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THE UNIVERSITY OF ALBERTA

ANALYSIS AND APPLICATION OF GROWTH MODELS TO BEEF CATTLE

BY

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A THESIS

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ABSTRACT

Four exponential growth functions: Richards, Brody, Bertalanffy and Logistic were fitted to unadjusted data from six breed populations and to data adjusted for year and age of dam effects for two populations. Growth curves and parameters characteristic of each function were derived for each set of data.

Data for each breed population consisted of weight/age records over a period of 10 years from 1962-1971 obtained from the University of Alberta experimental breeding ranch in Kinsella.

The fit of the functions derived for each set of data were examined at birth, weaning, yearling, 20 months, 32 months, 44 months, 56 months (adult) and over all ages using R^2 values, mean prediction error estimates and residual variances. The degree of fit of the models in the two major populations the Hybrid (HY) and Hereford (HE) breed groups were studied in detail.

The Richards and Brody models described growth well over the entire trajectory as the R^2 values were high while mean prediction error estimates and residual variances were low. Adjusting the data for year and age of dam reduced the residual variances in all models and mean prediction error estimates in all but the Richards model.

The Richards model provided an accurate prediction of birth weight in all of the data set while the Brody model provided a variable fit. The Bertalanffy and especially the Logistic function were poor in predicting birth weight in all data sets. Weaning weight was almost always predicted well by the Brody and Richards models. During the intermediate ages from yearling to 44 months all functions predicted weight with relatively small errors with the exception of weight at 32 months of age at which time no function could adjust for a temporary weight loss due to winter stress characteristic at that age group. The functions repeatedly underestimated adult weight and only the Richards and Brody functions predicted adult weights with some accuracy.

Adjusting the data for year and age of dam significantly improved the fit of the Brody, Bertalanffy and Logistic functions at birth and the Richards at weaning in both HY and HE breed groups, while the fit of the Brody was improved at weaning in the HY breed group. The improved fit of the functions by adjusting the data were confined to ages prior to yearling and responses were not identical among breeds.

The Richards and Brody functions were consistent in predicting small and similar mean prediction error estimates

at each age, compared to the Bertalanffy and Logistic functions. The overall mean prediction error estimates based on the Richards function were small and uniform between breeds thus demonstrating an overall consistency of fit and was therefore considered as being ideal for comparing estimates of fitted parameters.

The asymptotes (A) fitted by the Richards and Brody functions were always higher than those fitted by the Bertalanffy and Logistic. The Bertalanffy and Logistic functions were characterised as converging rapidly at the asymptote as predicted adult weights and asymptotes were similar. Adjusting data reduced the asymptotes in both breed groups, the effects being marked in the fitted asymptotes of the Richards function applied to the Hybrids.

Based on the estimates of the maturing rate parameter (k) the Herefords matured faster than the Hybrids. The maturing rates of the other breed groups appeared to be proportional to the amount of British beef blood in the populations.

Correlations between the parameters (A) and (k) were always negative. Selection for increased growth rate at early ages (6 months and 12 months) should result in increased maturing rates. Early maturing animals with rapid growth rates prior to 1 year of age grew to small mature

weights, and late maturing animals with relatively higher growth rates at 18 months grew to larger mature weights. Animals heavier at inflection showed higher growth rates at early ages and lower growth rates at 18 months. Selection for higher absolute growth rates at some age would improve gain more at immediately adjacent ages as a correlated response and less when the ages were widely separated.

The four growth models could not accurately predict absolute growth rate over 4 periods as the observed gains were of a fluctuating type and the functions were of an exponential decay type.

The Richards and the simpler Brody models were particularly good in describing growth in all populations and are recommended as being useful and a knowledge of their predictive and descriptive properties promotes a better understanding of the growth process.

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1. INTRODUCTION

Growth in animals is in general the increase in body mass with time, and is influenced by a number of factors such as the genetic potential of the animal, its nutrition and environment.

An animal basically grows in two ways, either by cell proliferation in the tissues (hyperplasia) or by cell enlargement (hypertrophy). The former process assumes much importance during the pre-natal growth phase while the latter process along with intercellular accretion are regarded as major determinants of growth during the post-natal growth phase (Robinson, 1971).

Growth curves are weight-age curves which are usually plotted from birth to maturity on individuals or populations and are useful for describing growth patterns characteristic of biological types. A gross growth curve can reveal stages at which animals make rapid gains in weight as against periods when growth is slow or constant, (as shown by Brody, 1945) depending on the slope of the growth curve between two points on a time scale.

Growth curves can also be expressed in other forms such as cumulative, absolute or relative and "reflect lifetime inter-relationships between an animals' impulse to grow with age in all tissues and the environment in which these

impulses are expressed" (Fitzhugh, 1976). The idea of growth ie. change in biomass with respect to time, was given a mathematical description by Brody (1945) in his book, "Bioenergetics and Growth." According to Brody a cumulative growth curve followed a strict sigmoid shape with age and although variations occurred within ages due to the effect of the environment, the general shape was characteristically sigmoid. Brody divided the weight-age curve into three sections, 1) pre-natal, 2) post-natal self accelerating, and 3) post-natal self inhibiting phases; the latter two being described by two different equations. During the post-natal self accelerating phase, growth, measured by an increase in body weight, showed an exponential relationship with time, increasing at an accelerated rate. During the self inhibiting phase the growth process was slower and gains were made at a decreasing rate. The point, or period, where the self accelerating curve joined the self inhibiting curve was recognised by Brody as the point of inflection (POI) and considered as the point or stage of sexual maturity (puberty). In subsequent studies this point at which the velocity of growth changes was computed as being approximately the time an animal reaches one third of it's mature body weight (Fabens, 1965).

Following Brody's studies many other equations have

been used and developed among which the more important are the Gompertz, Logistic, Bertalanffy and the Richards. These functions have been applied to study patterns of growth in animal forms. Each growth equation has its own characteristics and therefore may give a better fit on certain types of data. Most reports that have used a growth curve approach concentrate on the overall fit of the functions and correlations between fitted parameters, but a careful analysis of the fit of a growth curve at various ages has not been reported.

Therefore the present study was designed to evaluate the degree of fit of the growth equations - Bertalanffy, Brody, Logistic and Richards - to beef cattle growth data obtained from breed populations maintained at the University of Alberta ranch in Kinsella, with emphasis on their ability to describe growth and predict weights during certain pre-determined ages, some of which are of economical importance. The raw data as well as data adjusted to remove certain within age variation were used in the analyses.

The fitted parameters from each function were compared between populations and within functions to arrive at estimates of the asymptotes and maturing rates. Correlations between parameters both fitted and derived were calculated on the functions of best fit to study expected responses to selection. The average daily gains based on

the predicted weights from each growth function were compared with observed average daily gains to determine the efficiency of growth curves in predicting this trait.

2. LITERATURE REVIEW

A review of literature on growth curves reveal basically two types of equations. The first type of equation, which is actually a part whole relationship (allometry), was used by Huxley (1932) where (Y) was equal to bX^k in which (b) and (k) were constants and (Y) the weight of some organ (part) and (X) the body weight (whole). Huxley (Cheek, 1968) considered growth as a process of self multiplication and the rate of growth of an organism growing equally in all parts was at any moment proportional to the size of the organism.

A second type of growth curve was demonstrated by Brody in 1932 (Weinbach, 1941) to be of an exponential nature and applied to human growth from birth to puberty. Since the publication of Brody's book "Bioenergetics and Growth" in 1945 many other exponential equations describing weight-age relationship were developed, four of which were the Bertalanffy (Bertalanffy, 1957), Richards (Richards, 1959), Logistic (Nelder, 1961) and the Gompertz (Laird, 1965). These functions have been commonly used to describe growth of many animal species.

2.1 Brody function

The first exponential equation to be developed, given a

mathematical description and applied to various animal species was by Brody (1945). Two equations were derived, 1. the self accelerating and 2. self inhibiting. The self inhibiting equation of the Brody function is a 3 parameter model with (A), (B) and (k) as the fitted parameters, referred to as growth constants (Brody, 1945). The self inhibiting equation is correctly applied post inflection and has wide applicability in describing growth of different species (Brody, 1945).

The two equations are:

1. $Y = ae^{-kt}$

2. $Y = A(1 - Be^{-kt})$

where,

Y = weight in relation to time, t.

a = Y intercept

e = log base e

B = integration constant established by the values of Y and t and adjusts for the situation when $Y \neq o$;

A = asymptote as $t \rightarrow \infty$

k = instantaneous relative growth rate (Brody, 1945)

In equation 1 the growth rate (k) was computed in relation to the gains already made hence (k) was positive, and in

equation 2 growth rate was computed in relation to the gains yet to be made (A-Y) and (k) was negative (Brody, 1945).

2.2 Bertalanffy function

The Bertalanffy function is another 3 parameter exponential function used to describe growth (Bertalanffy, 1957).

$$Y = A(1 - Be^{-kt})^3$$

where, Y, B, A, k and e are as described in 2.1. The function is similar to the Brody function and has a fixed point of inflection at 8/27 A (Bertalanffy, 1957). Fabens (1965) described the Bertalanffy curve as being of a decaying exponential type and considered it to have a wide application in biology.

2.3 Richards function

The Richards function was originally an extension of the Bertalanffy function and was first applied to describe plant growth (Richards, 1959).

The function is given as follows:

$$Y = A(1 - Be^{-kt})^M$$

where, Y, B, A, k and e are as described in 2.1 and M = the variable shape parameter. Like the other growth functions the Richards contains the three parameters (A), (B) and (k)

and in addition a fourth parameter (M) which is referred to as a variable shape parameter. The value of (M) can vary, and determines the point of inflection in relation to the asymptotic weight (A) (Richards, 1959). The Richards model is a generalized function and the Brody, Bertalanffy and Logistic function have been considered as special cases of the Richards (Fitzhugh, 1976).

2.4 Logistic function

The Logistic function is a 3 parameter exponential function and the procedure of fitting it is described by Nelder (1961). The function is similar to the Brody function and has the following format.

$$Y = A(1 + Be^{-kt})^{-1}$$

where, Y, B, A, k and e are as described in 2.1 The Logistic function contains the parameters (A), (B) and (k) and its point of inflection is fixed at 0.5 A. Its use has been demonstrated on mice data by Rutledge et al. (1972).

2.5 Gompertz function

Laird (1966) has shown that the post-natal growth for a variety of animals such as birds and mammals undergoes an exponential decay in specific growth rates with time. The Gompertz function has been used to describe growth of mice (Laird and Howard, 1967; Laird, Tyler and Barton, 1965;

Laird, 1965), and reported to fit better than the Logistic function when applied to growth of dairy cattle (Vieira and Hoffman, 1977).

2.6 General

Growth functions can be fitted to many types of data classified as static, cross sectional, longitudinal, mixed cross sectional or mixed longitudinal (Cock, 1966; Tanner, 1951). Data of a longitudinal type provided a relevant description of the patterns of growth, as weight for age data is recorded throughout an animal's life and a complete set of experimental measurements is made available for every individual at each stage or age. In addition to providing the data yielded in a static or cross sectional type, it provides information on individual variations in growth (Cock, 1961; Fitzhugh, 1976). This type of data was recognised as being most appropriate for describing growth in a growth curve analysis (Fitzhugh, 1976).

In summary, the basic fitted parameters derived by the 3 parameter models, Brody, Bertalanffy and Logistic functions are (A), (B) and (k). The Richards function a four parameter model also computes a value for (M) which determines the point of inflection.

2.7 Application of growth functions

The Brody function has been used to describe and predict weights, and compare growth parameters of many species of animals and its wide application in biology has been documented (Brody, 1945).

Brown et al. (1972ab, 1973) fitted the Brody equation to female Hereford and Angus growth data and obtained estimates of mature weight and maturing rates. The authors stated that although the growth curve smoothed out the fluctuating data points, the function was adequate in describing growth. Their results were not difficult to interpret although the genetic and phenotypic correlations in relation to the parameter (k) differed considerably between breeds.

The pre- and post-inflection equations of the Brody function were used to study growth patterns in Black tailed deer (Bandy et al., 1970). They also determined the point of inflection in races of Black tailed deer as the pre-inflection function followed a straight line up to the point of inflection. The authors questioned the adequacy of the Brody function in describing growth rates in absolute terms but were satisfied that it was efficient for inter-racial comparisons. Lerner (1939) stated that "the pre-inflection growth curve although widely used with many excellent

results is limited in its value to small areas of a growth curve" (Baker, 1944). Brown (1970) described the Brody function as one which provided an excellent fit to the data points in beef cattle but did not permit an in depth study of growth properties.

Parks (1970ab) developed and used an extension of the Brody function: a) relating the biomass of an animal to feed consumption, b) cumulative feed consumption to age and c) a combination of the first two equations, biomass to age.

Taylor (1968) used the Brody and Gompertz growth equations on data described by Brody (1945) and Laird (1966) to demonstrate the proportionality between the time a species takes to mature and its mature weight. The time a species takes to mature was computed as the 0.27th power of its mature weight; the two growth equations and data giving similar values (Taylor, 1968). Comparing different species in relation to their maturing rates Taylor (1968) found birds matured faster than mammals, which tends to support his statements in an earlier paper relating species size and time taken to mature.

The Richards function plus the Bertalanffy, Logistic and Gompertz (Fox, 1970) have been applied to study growth patterns of ewes. The Richards function was considered best in describing growth although the parameter (M) which

determines the point of inflection was negative, thereby limiting the study of the inflection parameters. Brown et al. (1976) and Brown (1970) found the Richards was better than the Brody, Gompertz, Bertalanffy and Logistic functions in providing a good fit to beef cattle data.

The Gompertz function was cited as being adequate in describing growth of beef cattle (Cartwright and Joandet, 1969). The authors stated that the parameters derived had biological meaning and could be related to other traits. Laird et al. (1966) and Laird and Howard (1967) used the Gompertz function to describe growth data for mice and analyse strain differences. The authors state that the Gompertz function described growth adequately.

Growth curves of the Logistic and Gompertz type have been applied to human height data and a close correspondence between observed and predicted values found (Marubini et al., 1971). The Logistic function was applied to study the growth among mice selected for low and high body weights (Eisen et al., 1969). The authors reported that the Logistic function provided the best fit and description of growth among lines of mice although the other equations that were tried could have detected differences between lines. Rutledge et al. (1972) compared the Logistic and Richards functions as applied to mice and concluded that the former offered a better fit to the data. A growth function of the

Logistic type has been applied to broiler chickens and appears to be efficient in describing growth characteristics of birds on three commercial farms (Liljedahl, 1970). The use of growth equations in describing growth of birds was shown by Ricklefs (1968).

The basic biological parameters that growth curves can deduce are size and rate parameters (Fitzhugh, 1976). He stated that the first parameter (A) establishes the position of the individual or group in the general size space at a given reference age, usually maturity. The second parameter (k) concerns growth rate to body size. When the size parameter refers to mature size this parameter defines average maturing rate (Fitzhugh, 1976). A third group of parameters referred to as the inflection parameters are often determined in studies. The point of inflection, or the inflection parameter as it is sometimes called, is that point at which growth rate is maximum (Brody, 1945; Brown et al., 1976). Weight at inflection (Y*) and time at inflection (t*) have been determined in several studies (Timon and Eisen, 1969; Bandy et al., 1970; Brown et al., 1976).

In addition other parameters such as the predicted absolute and relative growth rates and weighted absolute growth rates can be computed from the functions when the values for (A), (B), (k) and (M) are known (Richards, 1959;

Fitzhugh, 1976). On this basis in addition to comparing fitted growth constants already included in the function, derived growth rates can be compared between breed groups or populations (Eisen et al., 1969; Rutledge et al., 1972).

Brown et al., (1972a) stressed the importance of providing a true adult weight in the data as the value of (A) is underestimated whenever weights are not available up to full maturity. Thus, the fit of the model and derived parameters will be determined by the last weight observed in the data (Brown, 1970; Fitzhugh, 1976). Furthermore, when a growth curve approach is used to study the efficiency of selection for growth traits the entire growth curve should be considered rather than small segments (Brown, 1970).

All growth curves when applied to any form of fluctuating data tend to smooth out the irregularities (Brown et al., 1972a; Fitzhugh, 1976; Brown et al., 1976). Brown (1972a) reports that as fluctuations occur when field data are used a correction can be made for factors such as weight loss during parturition or lactation but difficulty arises in adjusting for the corrections when trying to interpret the data. Fitzhugh (1976) reported that adjustments for weight losses of cows after parturition overestimated the mature weight. Fitzhugh (1976) therefore suggested other alternatives such as skipping the overfluctuating data and using weights which conformed

closely to the prior weight in relation to a curve. This procedure however will lead to some subjectivity in the data. Brown (1970) as reported by Fitzhugh (1976) stated that simultaneous adjustment of data while fitting non linear models was computationally intractable and fitting models to unadjusted data seemed most appropriate.

The reports appearing in the literature utilizing a growth curve approach and the types of study reported are summarised in Table 1. Most authors cited have worked with growth functions that are of particular interest in this report, some restricting themselves to single functions while Brown et al. (1976) worked with all five functions of interest to beef production.

Table 1. A listing of growth function studies from the literature

Author/year	Species	Function(s)	Type of Study
Brody (1945)	Many	Brody	General application and derivation
Laird et al (1965)	Mice	Gompertz	Derivation, fitting and application
Laird (1965)	Man/mice	Gompertz	Application of specific growth rate to whole and part of body
Laird (1966)	Birds/mammals	Gompertz	Application to embryonic growth
Laird (1967)	Man	Gompertz	Application and discussion of the human growth curve
Ricklefs(1967)	Birds	Brody Logistic Gompertz	Application and evaluation of growth rates in migratory birds
Kidwell et al (1969)	Mice	Gompertz	Analysis of hybridity between crosses of inbred lines
Timon et al. (1969)	Mice	Richards Logistic	Fitting, h^2, correlations between and within parameters and functions
Eisen et al (1969)	Mice	Bertalanffy Richards Logistic Gompertz	Fitting and comparison of the fit of each function
Rutledge et al. (1972)	Mice	Richards Logistic	Application, fitting and correlations between parameters and functions in a cross fostering study
Eisen (1976)	Mice	All	General review
Joandet et al (1969)	Beef cattle	Gompertz	Application, fitting, economics
Fox (1971)	Ewes	Bertalanffy Richards Logistic Gompertz	Application, fitting, h^2, and correlations between parameters
Fitzhugh (1976)	Many but with special reference to beef cattle	All	A review of growth curve analysis and an alternative approach to study growth
Brown (1970)	Beef cattle	Brody Bertalanffy Richards Logistic Gompertz	Fitting, application to cattle growth, correlation between parameter estimates
Brown et al (1972)	Beef cattle	Brody	Application, fitting, discussion on maturing rates between breeds and sexes
Brown et al (1976)	Beef cattle	Brody Bertalanffy Richards Logistic Gompertz	Application, fitting, discussion of parameter estimates. Correlations between parameters and between functions

2.7.1 Heritabilities and correlations between parameters and functions

The heritability estimates of the fitted parameters (A) and (k) are shown in Table 2, listed by author, species and function.

The heritability of the asymptotic weight appears to be high in the studies reported by Timon and Eisen (1969) and Fox (1970) with the exception of an estimate based on the Richards function in the latter study. Lower heritabilities were reported by Brown et al. (1972a). Also Brinks et al. (1964) and Calo et al. (1973) have reported higher heritability values for mature weight with actual data.

The parameter (k) which is the maturing rate showed a range in the heritability values from 0.30-0.76. There appears to be a difference between the heritability values computed from the Richards and Logistic functions (Timon and Eisen, 1969). This difference was attributed to the increased individual variation in the parameters of the Richards function (Timon and Eisen, 1969). In the same study genetic and phenotypic correlations between functions, in relation to the same parameter were computed and the genetic correlation between the (k) values estimated by the Richards and Logistic functions was 0.0, while the correlation with respect to (A) was 0.98. Timon and Eisen

Table 2. Heritability estimates of fitted parameters (A) and (k) by author, species and function

Author/year	Species	Function(s)	Heritability (A)	Heritability (k)
Timon et al (1969)	Mice	Richards	0.66 ± 0.15	0.30 ± 0.14
		Logistic	0.76 ± 0.15	0.76 ± 0.15
Rutledge (1972)	Mice	Richards	0.34	0.36
		Logistic	0.18	0.00
Fox (1970)	Ewes	Logistic	0.83 ± 0.16	0.42 ± 0.15
		Bertalanffy	0.80 ± 0.16	0.56 ± 0.16
		Gompertz	0.80 ± 0.16	0.54 ± 0.16
		Richards	0.39 ± 0.15	0.31 ± 0.15
Brown et al (1972a)	Beef cattle	Brody (HE)	0.34 ± 0.25	0.33 ± 0.25
		Brody (AN)	0.21 ± 0.21	0.75 ± 0.33

HE - Hereford; AN - Angus

(1969) suggest that the two functions may be estimating different traits.

The inflection point in cattle has been estimated as between 6-18 months of age (Fitzhugh, 1976). Timon and Eisen (1969) reported heritability values approximating 1.0 for the age at the point of inflection (t*) and suggest that most of the variation is thus of an additive type. Rutledge et al. (1972) reported heritabilities of 0.08 and 0.05 for (t*) based on the Logistic and Richards functions. The authors attributed the low values largely to post-natal maternal influences. Heritability estimates of 0.86 for the weight at the point of inflection (Y*) have been observed in mice based on the Richards function (Timon and Eisen, 1969).

The heritability value of the parameter (B), an integration constant, is high and Brown et al. (1972a) suggested that early weight changes were thus highly heritable.

Two forms of correlation studies are reported in the literature, one restricted to correlations between parameter estimates based on the same function (Eisen et al., 1969), and the other involving correlations between functions with respect to the same parameter (Brown et al., 1976; Timon and Eisen, 1969; Rutledge et al., 1972).

Correlations between (A) and (k) are shown in Table 3.

Table 3. Correlations between fitted parameters (A) and (k) by author, species and function

Author/year	Species	Function	Genetic	Phenotypic	Residual
			Correlations between (A) and (k)		
Timon et al (1969)	Mice	Richards	-0.29 ± 0.30	-0.41	
			-0.34 ± 0.21	-0.40	
Eisen et al (1969)	Mice	Logistic 1	-0.28 ± 0.57	-0.20	
		2	-0.47 ± 0.46	-0.21	
		3	-0.76 ± 0.50	-0.43	
Rutledge et al (1972)	Mice	Richards		-0.38	
		Logistic		-0.30	
Brown et al (1972a)	Beef cattle	Brody HE	-0.95 ± 0.15	-0.72 ± 0.07	
		AN	-0.29 ± 0.15	-0.62 ± 0.13	
Brown et al (1976)	Beef cattle	Richards		-0.64 ± 0.14	-0.60
		Brody			-0.72
		Bertalanffy			-0.52
		Logistic			-0.56
		Gompertz			-0.66

1, 2 & 3 refer to lines of mice; HE - Hereford; AN - Angus

All correlations, genetic, phenotypic and residual between (A) and (k) were negative, ranging from -0.20 to -0.95 indicating that animals with higher maturing rates (k) reached lower mature weights (A) (asymptotes). This biological phenomenon is characteristic among species and growth functions. Fitzhugh and Taylor (1971) in an alternate approach to the study of growth have arrived at similar conclusions about the relationship between maturing rates and mature weight in beef cattle.

In the studies reported by Brown et al. (1972a) and Eisen et al. (1969) there appears to be a difference in the relationship between (A) and (k) with respect to breeds or lines. In the study reported by Eisen et al. (1969) three lines of mice were studied and the genetic correlations between (A) and (k) were low in the first, medium in the second and high in the third line. Brown et al. (1976) recognised some degree of independence of the parameters (A) and (k) within breeds and suggests that this genetic antagonism can be partially overcome by cross breeding. In the report by Brown et al. (1976) six breed groups were studied and although the Richards (k) value was 87% greater in one breed group compared to the other, there was only a 2% decrease in the asymptotic weights. Brown et al. (1976) suggested that due to the variation in the relationship between breeds, the rate of maturing (k) may be amenable to

genetic change.

Correlations between parameters other than (A) with (k) from four studies are presented in Table 4, classified by species and function.

Correlations between the inflection parameters (Y*) and (t*) and size parameter (A) were reported in several studies (Timon and Eisen, 1969; Rutledge, 1972; Brown et al., 1976). The phenotypic correlations between (A) and (t*) based on the Logistic functions (Eisen et al., 1969; Timon and Eisen, 1969; Rutledge et al., 1972) were positive ranging from approximately 0.3-0.6. Phenotypic correlations between the same two traits based on the Richards function were negative with values of -0.10 (Timon and Eisen, 1969) on mice and -0.61 (Brown et al., 1976) on beef cattle. However, in the first study (Timon and Eisen, 1969) a positive genetic correlation of 0.49 was reported. Positive phenotypic correlations between (A) and (Y*) were observed by both Brown et al. (1976) and Timon and Eisen (1969) suggesting that animals heavier at inflection are also heavier at maturity. Furthermore, strong positive correlations between body weights at different ages are shown by Fitzhugh and Taylor (1971), Brinks et al. (1964) and Smith et al. (1976).

Based on the Logistic function, both genetic and

Table 4. Correlations between parameter estimates by author, species and function

Author/year	Species	Function	Correlations					
			(A) and (t*)		(A) and (Y*)		(k) and (t*)	
			G	P	G	P	G	P
Timon et al (1969)	Mice	Richards	0.49	-0.10	0.39	0.14	0.77	0.60
		Logistic	0.28	0.35			-0.63	-0.63
Eisen et al Legates (1969)	Mice	Logistic 1	0.40±.37	0.31			-0.69±.47	-0.73
		2	0.28±.31	0.43			-0.79±.36	-0.77
		3	0.44±.37	0.58			-0.73±.52	-0.72
Rutledge et al (1972)	Mice	Richards		-0.07				
		Logistic		0.33				
Brown et al (1976)	Beef cattle	Richards		-0.61±.12		0.64±.14		

1,2 and 3 refer to lines of mice
G - Genetic; P - Phenotypic

Table 4. Cont'd

			Correlations					
			(k) and (Y*)		(t*) and (Y*)		(A) and (AGR)	
Author/year	Species	Function	G	P	G	P	G	P
Timon et al (1969)	Mice	Richards Logistic	0.74	0.66	0.85	0.85	0.42	0.31
Eisen et al (1969)	Mice	Logistic 1 2 3					0.77±.50 0.26±.54 0.58±.46	0.57 0.51 0.57
Rutledge et al (1972)	Mice	Richards Logistic						0.34 0.45
Brown et al (1976)	Beef cattle	Richards		0.01±.27		-0.11±.22		-0.23±.21**

1,2 and 3 refer to lines of mice
**Calculated absolute growth rate at the point of inflection
G - Genetic; P - Phenotypic

Table 4 Cont'd

Author/year	Species	Function	(k) and (AGR) G	(k) and (AGR) P	(A) and (M) G	(A) and (M) P
Timon et al (1969)	Mice	Richards Logistic	-0.14	0.28	-0.11	-0.33
Eisen et al (1969)	Mice	Logistic 1 2 3	0.83±.51 0.73±.46 0.09±.56	0.69 0.72 0.48		
Rutledge et al (1972)	Mice	Richards Logistic		0.44 0.71		-0.34
Brown et al (1976)	Beef cattle	Richards		0.46±.20**		-0.33±.20

1, 2 and 3 refer to lines of mice
**Calculated absolute growth rate at the point of inflection
G - Genetic; P - Phenotypic

phenotypic correlations between the maturing rate parameters (k) and the time of inflection (t*) were negative, the values ranging from -0.46 to -0.8 (Timon and Eisen, 1969; Eisen et al., 1969; Rutledge et al., 1972); however, correlations (rg and rp) between the same two functions based on the Richards were positive, the values ranging from 0.23-0.77 (Timon and Eisen, 1969). Conversely negative correlations between the two traits observed by Brown et al. (1976) among beef cattle, suggested that early maturing animals reached their inflection age early. Positive correlations between (k) and (Y*) were observed by Timon and Eisen (1969) whereas there was no apparent correlation between the same two parameters in the study by Brown et al. (1976).

Although among mice there appears to be a strong phenotypic correlation between the time of inflection (t*) and weight at inflection (Y*) (rp=0.85) (Timon and Eisen, 1969). Brown et al. (1976) reported that in beef cattle the weight at inflection showed no relationship to the age at inflection.

In summary, correlations between the size parameter (A) and rate parameter (k) and the inflection parameters (t*) and (Y*) appear to be specific to each function as each equation determines a different inflection point. Within each function the point of inflection is determined by the

function itself rather than the genotype of the animal (Fitzhugh, 1976).

Genetic and phenotypic correlations between (A) and absolute growth rate (AGR) in Table 4 were positive, based on the Richards function the values ranged from 0.31-0.42 (Timon and Eisen, 1969). Similar positive correlations were observed by Eisen et al. (1969) and Rutledge et al. (1972). Negative correlations were reported by Brown et al. (1976) between mature weight (A) and absolute growth rate (AGR) at the point of maximum growth ie. inflection. Positive phenotypic correlations between (k) and (AGR) suggested that animals with lower maturing rates (ie. late maturing) showed slower growth rates (Brown et al., 1976; Rutledge et al., 1972). Brown et al. (1976) suggested that, based on the Richards function a negative association between (A) and (AGR) and a positive association between (k) and (AGR) indicated early maturing animals had larger gains at inflection but grew to smaller adult weights. In all studies the correlations between (A) and (M) were negative suggesting that heavier animals at inflection reached heavier adult weights (Brown et al., 1976).

The second type of correlation observed in growth curve studies are those between functions within a parameter (Timon and Eisen, 1969; Brown et al., 1976). The general conclusions are that parameter estimates of functions with

similar biological interpretations are positively correlated, especially the asymptotes but these estimates are often smaller than expected (Fithugh, 1976). Fitzhugh (1976) further adds that similar parameters from two models may not measure the same biological phenomena.

2.7.2 Alternate growth analysis

Fitzhugh (1974, 1976) stated that most growth models assumed growth is a uniform monotonic increasing function with time. Furthermore, he adds that all growth functions are insensitive to irregular spacing of size or weight-age points and this determines not only their fit but also the accuracy; even when animals are weighed at regular intervals, the intervals are irregular with respect to physiological age and production status. Fitzhugh (1976) stated that when working with larger animals under field conditions, fitting an appropriate growth equation smooths out the irregularities in the actual curve and thereby overides the variation due to factors such as climate, level of feeding and nutrition, condition or production level, thereby possibly obscuring some of the more important genetic and environmental phenomena. With some of these concepts in mind, Fitzhugh and Taylor (1971) and Fitzhugh (1974, 1976) proposed an alternative two component model, referred to as an "equation-free analysis of growth curves",

for irregular data which preserves the variation in the original observations. Taylor (1965) stated that it has long been recognised there is a strong tendency for animals with larger mature weights to take a long time to mature. Taylor (1968) deduced a relationship equating the time taken to achieve a certain proportion of the mature weight to a maturing interval, and a degree of maturity. When weight (Y) at some point in time is expressed as some proportion (P) of its mature weight, then the proportion Y/A where (A) is the mature weight, is referred to as the degree of maturity (U) (Taylor, 1965). According to Fitzhugh (1976) the degree of maturity parameter (U) and the parameter (k) from non linear models are alternate ways of characterising animals for being early or late maturing. The parameter (U) in addition does not have the disadvantage of (k) as it can be applied to small areas of the growth curve, or to economically important stages during growth and need not be computed from birth to maturity (Fitzhugh, 1976). The method of analysis has been used by Smith et al. (1976a, 1976b) to study growth traits.

3. GROWTH FUNCTIONS

Table 5 lists the Richards, Brody, Bertlanaffy and Logistic growth equations and some of their properties considered in this report. The four functions were similar in their computational formulae and had been used to describe beef cattle growth. The parameters or traits and the appropriate codes are presented in Table 6.

3.1 Interpretation of growth curve parameters

The fitted parameters obtained from a growth curve analysis are (A), (B), (k) and (M). Other derived parameters such as the weight at point of inflection (Y*), age at point of inflection (t*) degree of maturity (u) and absolute growth rate (AGR) are of interest and can be interpreted biologically.

A major parameter each growth function describes is (A) the asymptotic weight which is considered to be a measure of mature weight; the value of (A) largely depends on the value chosen as the adult or mature body weight in the data. The value of (A) is computed as time (t) approaches infinity. Brown et al. (1976) stated that "the asymptote more nearly represents mature weight at a constant condition relative to the individuals norm for body composition under a given production environment rather than would a single weight",

Table 5. Growth functions, formulae and properties

Function	Formulae	Asymptote	Maturing rate	Shape Parameter	Weight at POI (Y^*)	Time of POI (t^*)	Growth rate dy/dt
Richards	$Yt=A(1-Be^{-kt})^{M}$	A	k	M	$A(M^{1}/1-M)$	ln MB/k	$MkYt(Be^{-kt}/1-Be^{-kt})$
Brody	$Yt=A(1-Be^{-kt})$	A	k	1	-	-	$kYt(Be^{-kt}/1-Be^{-kt})$
Bertalanffy	$Yt=A(1-Be^{-kt})^{3}$	A	k	3	0.296 A	ln 3 B/k	$3kYt(Be^{-kt}/1-Be^{-kt})$
Logistic	$Yt=A(1+Be^{-kt})^{-1}$	A	k	-1	0.5 A	ln B/k	$kYt(Be^{-kt}/1+Be^{-kt})$

Table 6. Explanation of symbols

Parameter, Trait or Effect	Code	Units
Asymptote	A	kg
Maturing rate	k	%/day
Integration Constant	B	-
Shape Parameter	M	-
Exponent	e	-
Time	t	days
Absolute Growth rate dy/dt	AGR	kg/day
Weight at Inflection	Y*	kg
Time of Inflection	t*	days
Weight	Y	kg
Weight Predicted	$\hat{Y}$	kg
Degree of Maturity	U	%
Year	YR	-
Age of dam	AD	months
Birth weight of calf	BW	kg
Mean prediction error	MPE	%

or a characterization of the mature body weight of a breed group or population.

The value (k) is the instantaneous relative growth rate computed from birth to weaning (Brody, 1945). It was also considered as growth rate relative to mature size and was referred to as the maturing rate (Taylor, 1965; Brown et al., 1972ab; Brown et al., 1976). In the present analysis the maturing rate was expressed as percent per day, as the time intervals were presented on a daily basis in the data. The values of (k) based on the same function are comparable between breeds although comparisons of the parameter between functions have been questioned (Timon and Eisen, 1969). A higher value of (k) computed over equivalent weight-age points would indicate a rapid maturing type whereas a lower value would indicate a slower maturing type. The parameter (k) has been used by Brody (1945) to compare growth patterns of different species. The use of it in the study of maturing patterns among cattle has been demonstrated by Brown et al. (1972a,b).

(B) is an integration constant adjusting for age and weight at birth and is used in the computation of other parameters such as absolute growth rate but in itself is not biologically interpretable.

Absolute growth rate (AGR) which is the slope of the

growth curve at a point (t) is the first derivative of each function. It can also be calculated using the derived parameters (A), (B), (k) and (M). Unlike in a usual analysis of daily gains, in a growth curve study absolute growth rate can be mathematically calculated at a point or stage in contrast to a period, or interval. Absolute growth rate in the present analysis was calculated as gain in kg/day. Derived life time gains such as absolute growth rates, maturing rates and relative growth rates could be obtained once the values of the fitted parameters are known.

The weight at point of inflection (Y*) and the age at the point of inflection (t*) can also be calculated on the Richards, Logistic and Bertalanffy functions once the values of (A), (B), (k) and (M) are known.

The ratio of (Y) to (A) in relation to time measures the degree of maturity which can be expressed as a percentage. Thus if,

$Y = A(1 \pm Be^{-kt})$ is a generalized growth curve

then $Y/A = (1 \pm Be^{-kt})$ =Degree of maturity (U)

From the preceeding discussion it becomes evident that a correct value representing the adult weight is exceedingly important as the maturing rate parameter (k) and the inflection parameters, are computed in relation to (A).

4. MATERIALS AND METHODS

4.1 Breed Groups

The 6 breed groups, codes and approximate breed composition of each breed group are shown in Table 7.

The Hybrid population was developed from three foundation breeds, namely Angus, Galloway and Charolais. This Hybrid line was started in 1961 and has been bred essentially as a closed line although some introduction of outside breeding continued up to 1970. At present the approximate breed composition of the Hybrid herd is 1/3 Angus, 1/3 Charolais, 1/4 Galloway and the remainder divided among several other breeds such as Hereford, Holstein, Jersey and Brahman introduced through foundation animals that were not pure (Berg, 1971, 1975).

The Hereford line was established in 1960 and has been maintained as a purebred line from its initiation with limited continued introduction from outside herds.

The four populations 100% BR, 75% BR, 50% BR 50%LD and 75% LB were derived from a line referred to as the crossbreds, in which the suitability of various combinations of Beef type x Beef type or Beef x Dairy types are being investigated. These populations will be collectively referred to as the XB groups.

Table 7. Breed groups, codes and approximate composition

Breed Group	Code	Approximate Composition
Hybrid	HY	33% Charolais, 33% Angus and 25% Galloway
Hereford	HE	100% Hereford
100% British Beef	100% BR	Crosses among Hereford, Shorthorn, Angus and Galloway
75% British Beef 25% Large Beef	75% BR	Crosses consisting of not more than 75% British Beef and 25% Large Beef (Charolais and Limousin)
50% British Beef 50% Large Dairy	50% BR 50% LD	Crosses consisting of 50% British Beef and 50% Large Dairy (Holstein, Brown Swiss, Simmental)
<50% British Beef and >50% Large Beef	75% LB	Crosses made up of more than 50% Large Beef breeds and the remainder consisting of British Beef mixtures

The data for the Hybrid and Hereford female populations were collected over a period of 10 years from 1962-1971 and for the four XB groups data was collected over a 6 year period from 1965-71 excluding 1969.

4.2 Breeding and selection program

Dams chosen to produce the subsequent generations are selected according to their reproductive ability, growth performance and general soundness. Selection on the basis of reproductive performance is strict. Cows are bred in the summer during a two month period, pregnancy tested during the winter and those that are not in calf at this time are culled. Calving usually occurs during spring the following year and is spread over a 2-2 1/2 month period. Calves are weaned at approximately 6 months and placed on a 140 day feed test over the winter. The feed test period is usually from November to mid March during which time all male calves are on full feed and females restricted feed.

Breeding bulls for populations are selected according to their pre-weaning and feedlot gain and about 5-7 bulls are used within each of the Hybrid and Hereford populations each year, one quarter of those selected being from the previous year and three quarters being yearling bulls. All heifers are exposed to the bulls for the first time when they are 15-17 months of age.

4.3 Feeding and management

The feeding and management practices of the breeding herds conform to that of commercial operations and the type of feed used during the experimental period depended on the availability of feed and cost. The winter feeding schedule is tabulated in Table 8 (Berg, 1971, 1973). During spring, summer and fall all dams were allowed access to free grazing.

4.4 Choice of data

All cows at Kinsella are weighed at intervals of approximately 2 months while heifers are weighed monthly.

In a preliminary study of the data 19 weight age points were plotted on a graph to observe the shapes of the growth curves and the general variation between weight age points. It was noted that the data was of a fluctuating type with much of the variation being observed between summer and winter weights. Based on visual examination, 9 of the 19 points were selected for growth curve analysis. The ages selected were: birth (0 days), weaning (6 months), yearling, 15 month weight, 18 month weight, 20 month weight, 32 month weight, 44 month weight and 56 month weight (adult). The last four weights were winter weights taken during the month

Table 8. Winter feeding schedule, Kinsella Alberta.

Year	Age and Type of Animal	Feeding Schedule
Prior to 1963	Cows and heifers	Winter grazing only
1963-1965	Cows and heifers	Winter grazing Barley soybean pellet containing 15% CP and 20,000 IU VIT A/LB, fed at 7 lb/head twice a week
	Heifers and 2 year olds	Additional hay 640 lb/heifer over wintering period standard
1964-65	Heifers and 2 year olds	Hay ration increased to 1300 lb/head over wintering period due to severity of winter
1965 to 1968	Cows and heifers	72 lb hay per week/head on Monday, Wednesday and Friday and a barley soybean pellet containing 29% CP and 70,000 IU Vit A/lb. Additional 27 lb rolled oats at 9 lb/day offered on alternate days Tuesday, Thursday and Saturday
	Wet Cows Heifers	In addition to above 5 lb straw on grain days and Sundays or when temperature was below 0°F
1968-1969	Cows and heifers	75% Straw replaced hay due to cost of hay.
	Heifers	Supplemental barley soybean fed as usual. Grain mixture containing 1 part barley and 3 parts rolled oats fed at 30 lb/head per week. Hay at 4 lb/day fed on grain days or when the temperature was below 0°F
1970 on	Heifers	Heifers given 4 lb/hay/day regardless of weather conditions in addition to straw and grain as above

of January of each year.

The number of animals used in each data set along with the number of observations at each age are shown in Table 9 for the six lines with unadjusted data and the Hybrid and Hereford lines with the adjusted data.

As the animals used each year were born over a 2-2 1/2 month period this variation existed at each age. Due to an overlap of weights at yearling a weight recorded at 11 months of age and a 15 month weight were regarded as the yearling weight in all populations. Thus, all breed groups had more observations recorded at yearling than at the preceeding weaning weight. In the adjusted Hybrid and Hereford data sets, some animals had an 18 month weight, while others had a 20 month weight whereas in the unadjusted data only a single animal weight represented 20 months. Consequently, more animals were analysed in the adjusted data sets. In the XB populations and the adjusted data two weights at 18 and 20 months of age were regarded as weight representing 20 months. The data analysed was of a longitudinal type where a set of observations was available on each animal depending on the length of time it remained in the herd.

4.5 <u>Analysis of data</u>

Table 9. Number of animals used in each breed and age group

		Number of Observations							
Data	Breed group	Birth	Wean	Yrl.	20 mon.	32 mon.	44 mon.	56 mon.	Number of animals
Unadjusted	Hybrid	203	203	398	177	158	142	128	203
	Hereford	144	144	274	126	107	89	67	144
	100% BR	34	34	52	45	25	13	12	34
	75% BR	56	56	93	70	39	22	12	56
	50% BR 50% LD	28	28	46	34	19	13	6	28
	75% LB	21	21	33	28	14	10	7	21
Adjusted	Hybrid	454	439	976	591	269	223	185	454
	Hereford	319	307	679	413	192	147	102	319

4.5.1 Unadjusted

Growth curves were fitted to a sample set unadjusted weight data from of 203 Hybrid and 144 Hereford dams. Similarly, growth curves were fitted to unadjusted weight age data the four XB groups using all available records.

4.5.2 Adjusted

Growth curves were fitted to adjusted data from the Hybrid and Hereford lines, the data adjusted for year effects and age of dam. All available records comprising 454 Hybrid and 319 Hereford females were used for the analysis.

Weights of the HY and HE breed groups from birth to 56 months were adjusted for year (YR). Weights from birth to 18 months were in addition adjusted for age of dam (AD) classified as 2, 3, 4, 5, 6-8 and ≥9 years. The model used was:

$$\hat{W}ijk = Wijk - Ci - Cj$$

where,

$\hat{W}ijk$ = adjusted weight

Wijk = the unadjusted weight of the ith year, jth age of dam and kth observation

Ci = least squares constants for years

Cj = least squares constants for age of dam

(Birth to 18 months)

where $i = 1,2 \ldots\ldots\ldots 10$

$j = 1,2 \ldots\ldots\ldots 6$

$k = 1,2 \ldots\ldots\ldots nij$

The fit of the Richards, Brody, Bertalanffy and Logistic equations, over all ages and at 7 weights which included birth, weaning, yearling, 20 months, 32 months, 44 months and 56 months (adult) were studied in detail using unadjusted and adjusted data.

4.6 Statistical procedures

4.6.1 Construction of growth curves

The four growth functions - the Richards, Brody, Bertalanffy and Logistic were fitted independently to each data set. A non-linear least squares programme BMD07R (BMD Health Services Computing Faculty UCLA) which used the Gauss Newton iterative procedure fitted the models to the data. The programme allowed a maximum of 100 iterations in the computation of each set of parameter estimates and was run with no constraints.

4.6.2 Estimation of overall fit

The accuracy of overall fitting was determined using

the square of the multiple correlation coefficient (R^2).

Because in non linear regression the deviation of observed minus predicted do not necessarily equal zero and because it was expected that at a particular age an equation may over or under fit, a measure of average relative deviation called mean prediction error (MPE) was developed.

$$\% \text{ MPE} = \sum_{i=1}^{n} (Yi-\hat{Y}i/Yi \times 100)/n$$

A lower MPE indicated a lower non symmetrical error or a symmetrical error of any size and a better relative prediction of weight.

Overall fit was also compared by calculating MPE over all 7 ages and by use of residual variance from a one way analysis of variance where differences between ages were removed.

4.6.3 Comparison of fit within age and between functions

The criterion used to determine the degree of fit of each function at each of the 7 ages was the mean prediction error estimate.

The MPE estimates computed from each growth function within an age class and breed group were compared by a 't' test to establish significant differences (Snedecor, 1962).

4.6.4 Comparison of fit between unadjusted and adjusted data

The mean prediction error estimates and residual variances were used to compare the fit of each growth function between the unadjusted and adjusted data over all ages from birth to 56 months and at 7 ages in the Hybrid and Hereford lines. The MPE based on each function were compared by a 't' test (Snedecor, 1962).

4.6.5 Analysis of the consistency of fit

The overall consistency of fit between breeds was determined by comparing the mean prediction error estimates within the same function. MPE estimates that were small and not significantly different between breeds provided a more consistent overall fit. A 't' test (Snedecor, 1962) was used to establish significance between means.

A Duncan's range test was applied to the mean prediction error estimates within each function for all sets of data to determine the uniformity of fit. The test was made to determine the significant differences among the estimated mean prediction errors over the 7 age periods.

4.6.6 Correlations among parameters

A random sample consisting of 50 Hybrids and Herefords each having a complete set of adjusted weights were used to calculate the correlations between (A), (B), (k), (M), (Y*), absolute growth rate at 6 (AGR6), 12 (AGR12) and 18 months (AGR18) based on the Richards function and parameters (A), (B), (k), (AGR6), (AGR12) and (AGR18) based on the Brody function. In calculating the correlations between the weight at point of inflection (Y*) and all cther parameters both fitted and derived 25 observations per set of data was used.

4.6.7 Analysis of absolute growth rates

The Richards, Brody, Bertalanffy and Logistic functions were fitted to the adjusted weight data from the Hybrid and Hereford lines. Weights were predicted at birth, weaning, yearling, 18 months and 56 months. Absolute growth rates/day (average daily gain) were calculated for the periods from birth-weaning, weaning-yearling, yearling-18 months and 18 months-56 months as a difference in weights divided by the time interval.

$$AGR/day = Y2-Y1/t2-t1$$

The observed gain per day and predicted gain/day based on each function were next compared within period using a

procedure by Gill (1977) designed to make a number of independent comparisons (Dunnett type) between means taking into account the heterogeneity of the variances.

$$SED = \sqrt{S_1^2/ni + S_2^2/ni}$$

$$MSD = t\ 0.01(SED)$$

where,

SED was the standard error of a difference

MSD was the minimum significant difference

S_1^2 and S_2^2 the variance of the observed and predicted

ni the number of observations

The MSD was compared with the difference between the observed and predicted means $(Y-\hat{Y})$ to establish significance.

The same statistical procedure was used to compare the observed and predicted mean gain over period based on the four growth functions for the adjusted data from the Hybrid and Hereford breed groups.

5. OBJECTIVES OF THE STUDY

The objectives of the study were to:

(1) evaluate the accuracy and consistency with which the Richards, Brody, Bertalanffy and Logistic functions predicted weight (degree of fit) over all ages and at seven ages from birth to maturity for several breed groups and data sets.

(2) determine the effect on degree of fit overall ages and at each age when data were adjusted for year and age of dam effects in the HY and HE breed groups.

(3) compare asymptotes (A), maturing patterns (k) and inflection parameters (Y*) and (t*) among the breed groups.

(4) evaluate the correlations between fitted and derived growth parameters using information from the two functions of best fit to estimate responses to selection.

(5) evaluate how accurately each growth function approximates absolute growth rates or average daily gains.

6. RESULTS AND DISCUSSION

6.1 Least squares estimates for adjusted data

The least squares constants used for adjusting the Hybrid and Hereford weight data for year and age of dam effects are shown in Tables 10 and 11. The year effects were variable and weights were adjusted accordingly. Adjusting for year removed part of the genetic and environmental trends. The results showed a gradual increase in the age effect as the age of dam increased.

6.2 Growth curves

Cumulative 'sigmoid' growth curves characteristic of each function fitted to the 8 sets of data are shown in Figures 1-8. The letters U and A refer to unadjusted and adjusted data respectively. The shapes of the Richard's and Brody curves were similar in all of the data sets. Furthermore, the two individual curves could not be separately identified in the 100% BR, 50% BR 50%LD, 75% LB and Hybrid A sets due to considerable overlap.

The Logistic function overestimated birth weight and underestimated adult weight and this feature was characteristic across all sets of data. The Bertalanffy and Logistic functions also showed a rapid convergence pattern to adult weight starting at approximately 750 days of age.

Table 10. Least squares constants for main effects (YR) and (AD) for adjusting Hybrid data

Main effect	Age								
(YR)	W0	W6	W12	W15	W18	W20	W32	W44	W56
1	-1.68	-11.50	-16.69	-15.31	-31.31	-7.82	-34.96	-10.23	14.76
2	-0.60	-8.35	-21.91	-32.72	-24.97	-34.20	1.84	19.83	-27.96
3	1.87	-12.41	-0.36	-13.12	-6.18	16.63	12.71	-21.37	7.08
4	0.34	-13.3	-4.32	-42.79	-12.95	-10.738	-33.06	-20.26	-24.35
5	0.78	5.91	24.20	24.08	17.17	-0.28	4.89	2.69	3.31
6	0.27	7.65	24.81	18.29	7.55	-5.41	-11.81	3.49	-5.94
7	-1.51	1.91	4.35	59.90	9.59	6.45	22.65	6.61	6.28
8	-0.89	8.90	4.84	6.59	22.04	6.86	-6.56	-8.76	13.74
9	0.48	11.03	-5.74	-2.05	10.60	6.60	12.57	1.66	5.31
10	0.93	10.23	-9.18	-2.36	8.45	21.90	31.71	26.33	7.75
(AD)									
2	-2.69	-7.94	-8.10	-2.85	-6.54				
3	-1.62	-10.29	-6.41	-10.69	-6.50				
4	-0.19	-3.50	-1.90	1.36	0.39				
5	0.24	5.10	2.47	2.01	1.10				
6-8	1.84	13.44	10.28	6.09	8.55				
>9	2.41	3.19	3.67	4.08	2.98				
Percent Reduction in variance	20.84	23.63	25.32	38.10	20.91	15.00	18.20	9.42	7.13

W=Weight

Table 11. Least squares constants for main effects (YR) and (AD) for adjusting Hereford data

	Age								
Main effect	W0	W6	W12	W15	W18	W20	W32	W44	W56
(YR)									
1	1.58	-9.06	-18.42	-17.77	-14.86	0.14	-27.64	-2.38	-12.94
2	0.49	-9.73	-28.28	-40.19	-24.95	-41.69	-0.56	29.36	-12.21
3	1.44	-4.27	0.83	-10.20	-5.40	15.80	14.72	-14.52	12.24
4	-0.69	-7.95	9.89	4.44	1.48	7.56	-20.90	0.41	-11.60
5	-1.21	8.44	19.74	16.17	7.00	-3.93	2.59	-9.06	-19.80
6	-0.70	3.96	7.83	-2.12	-2.72	-7.96	-2.22	5.53	-2.14
7	-1.16	12.04	16.22	67.60	18.51	6.38	12.38	-11.21	-16.76
8	-0.56	1.94	-1.40	-2.41	11.89	10.26	-13.40	-10.72	0.81
9	0.98	3.44	-8.44	-5.76	2.41	-2.82	19.67	9.15	40.95
10	-0.16	1.15	2.02	-9.75	6.63	16.23	15.36	9.45	-4.41
(AD)									
2	-3.87	-17.87	-18.03	-18.69	-17.40				
3	-1.62	-9.54	-6.30	-3.69	-5.57				
4	-0.83	-0.47	2.00	-0.67	0.37				
5	0.95	5.63	3.78	4.68	4.84				
6-8	2.10	14.21	14.58	9.44	9.45				
>9	3.24	8.05	3.97	8.93	8.29				
Percent reduction in variance	24.50	30.40	34.93	52.56	23.0	22.82	12.30	8.91	11.12

W=Weight

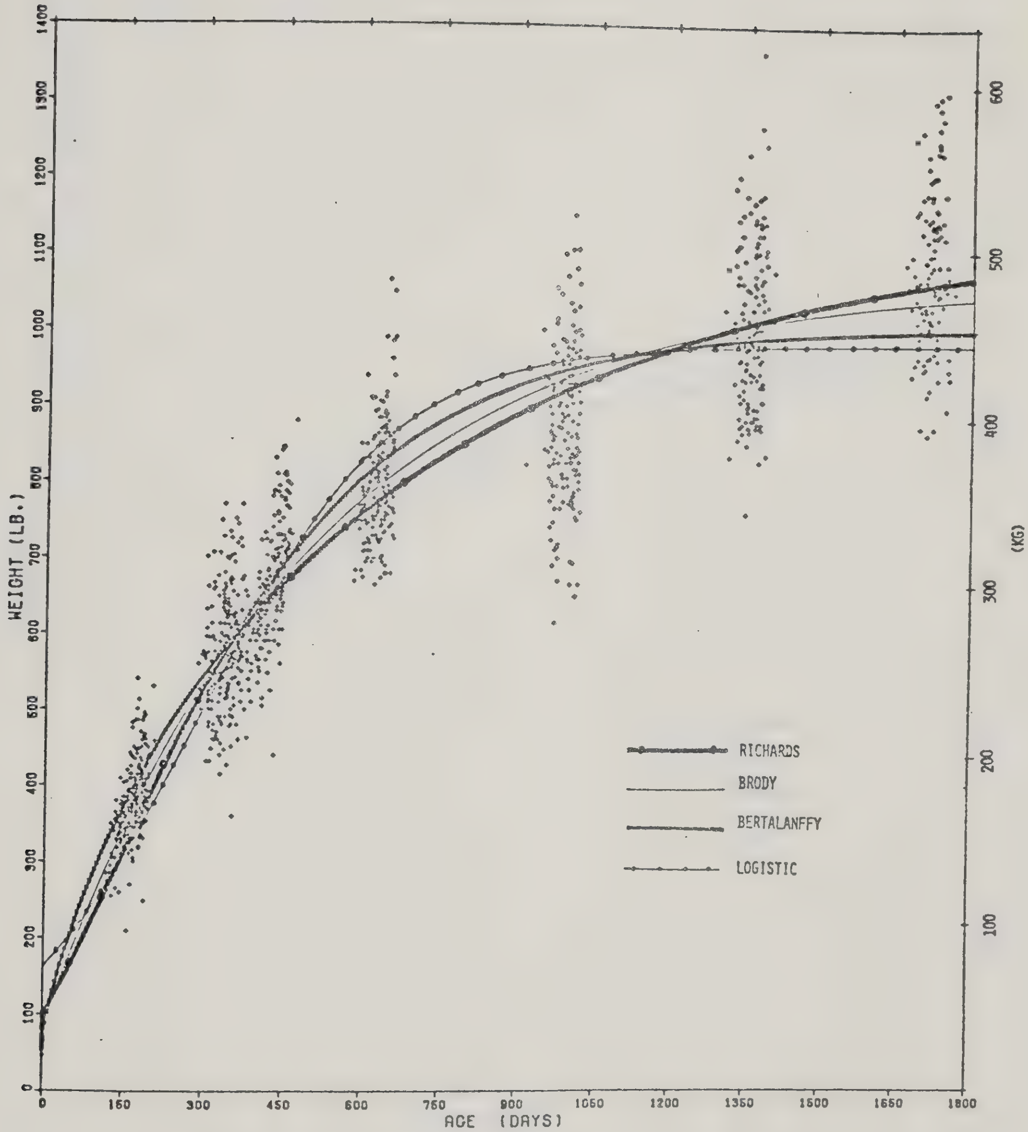

Fig. 1. GROWTH CURVES, WITH DATA FOR BREED HYBRIDS U

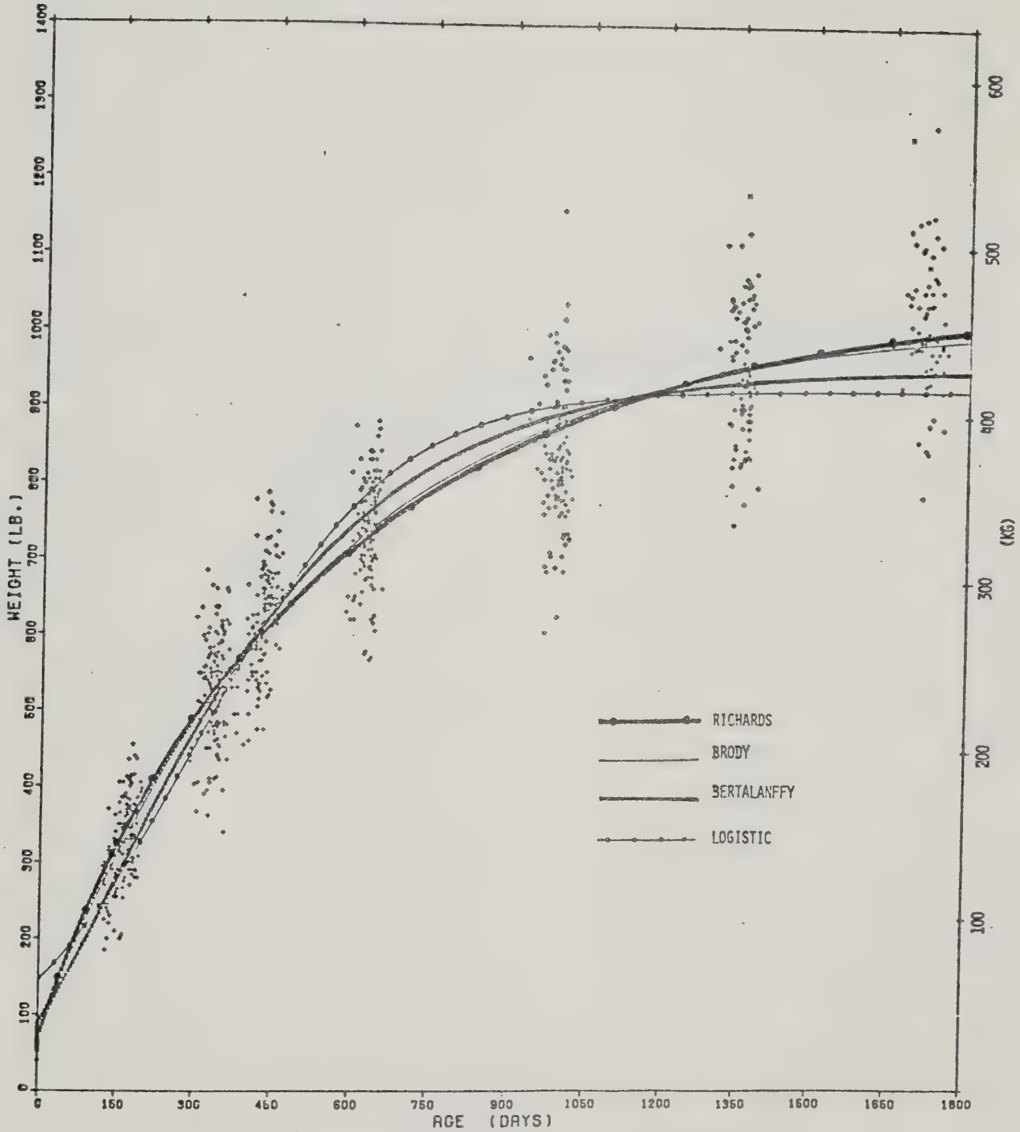

Fig. 2. GROWTH CURVES. WITH DATA FOR BREED HEREFORDS U

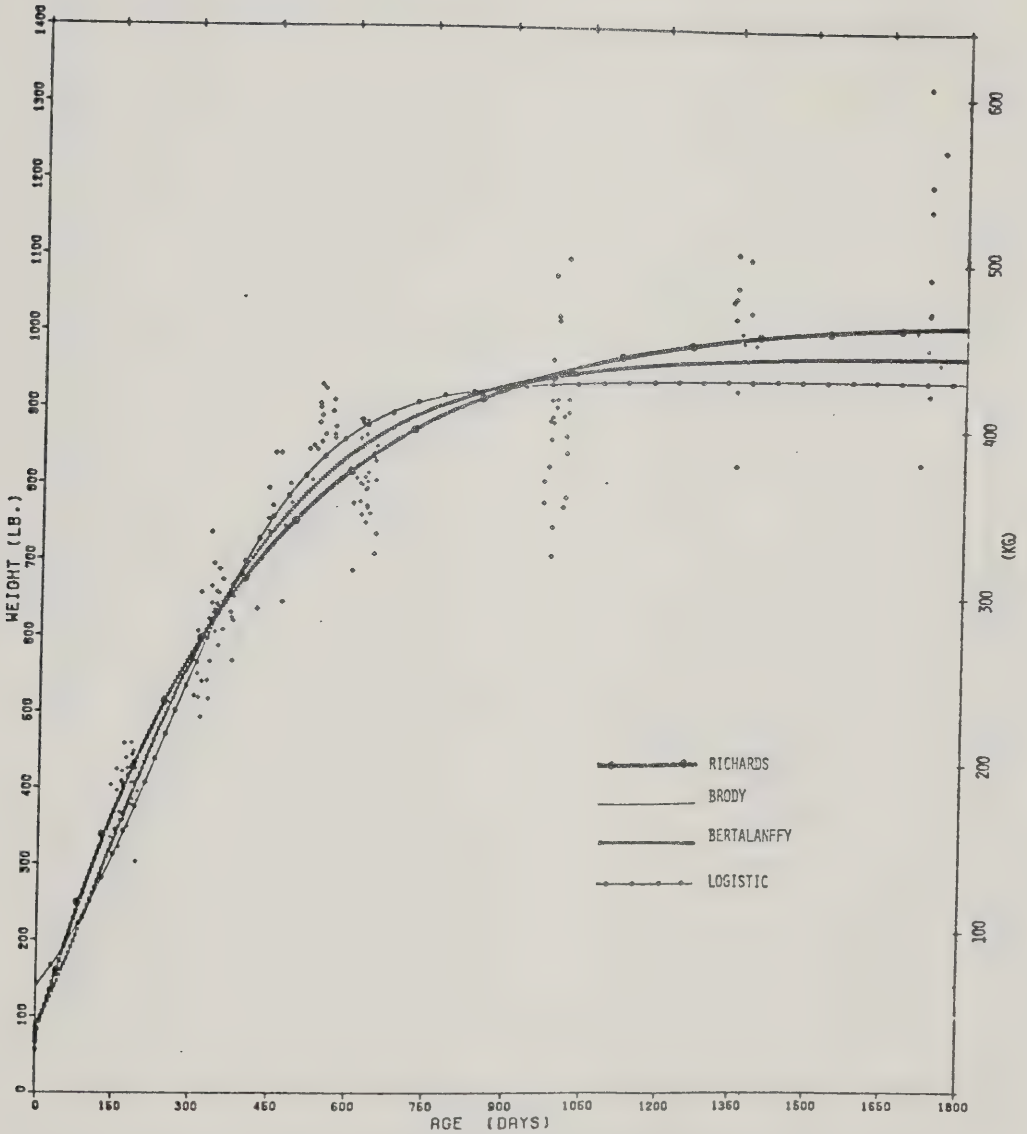

Fig. 3. GROWTH CURVES, WITH DATA FOR BREED BR 100%

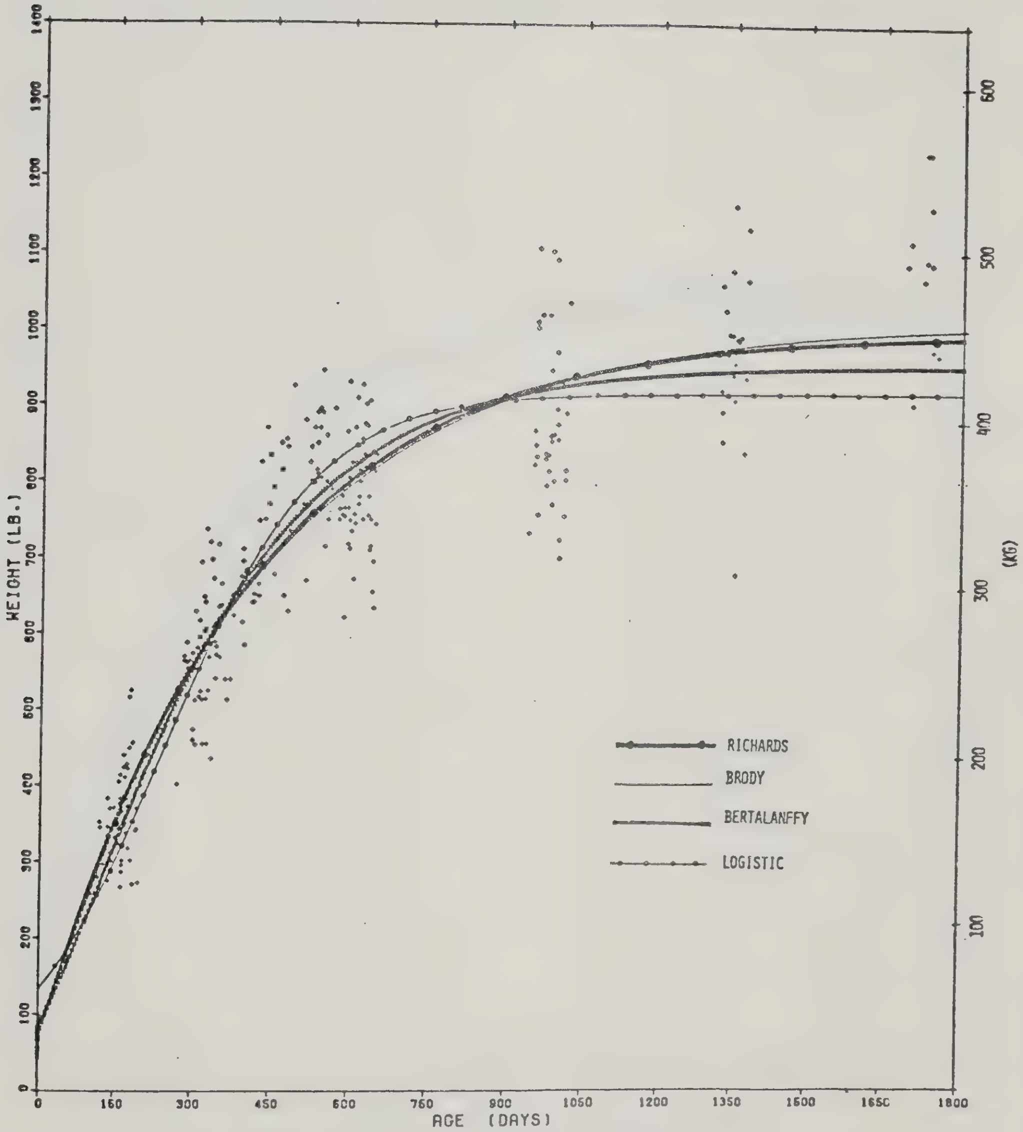

Fig. 4. GROWTH CURVES. WITH DATA FOR BREED BR 75%

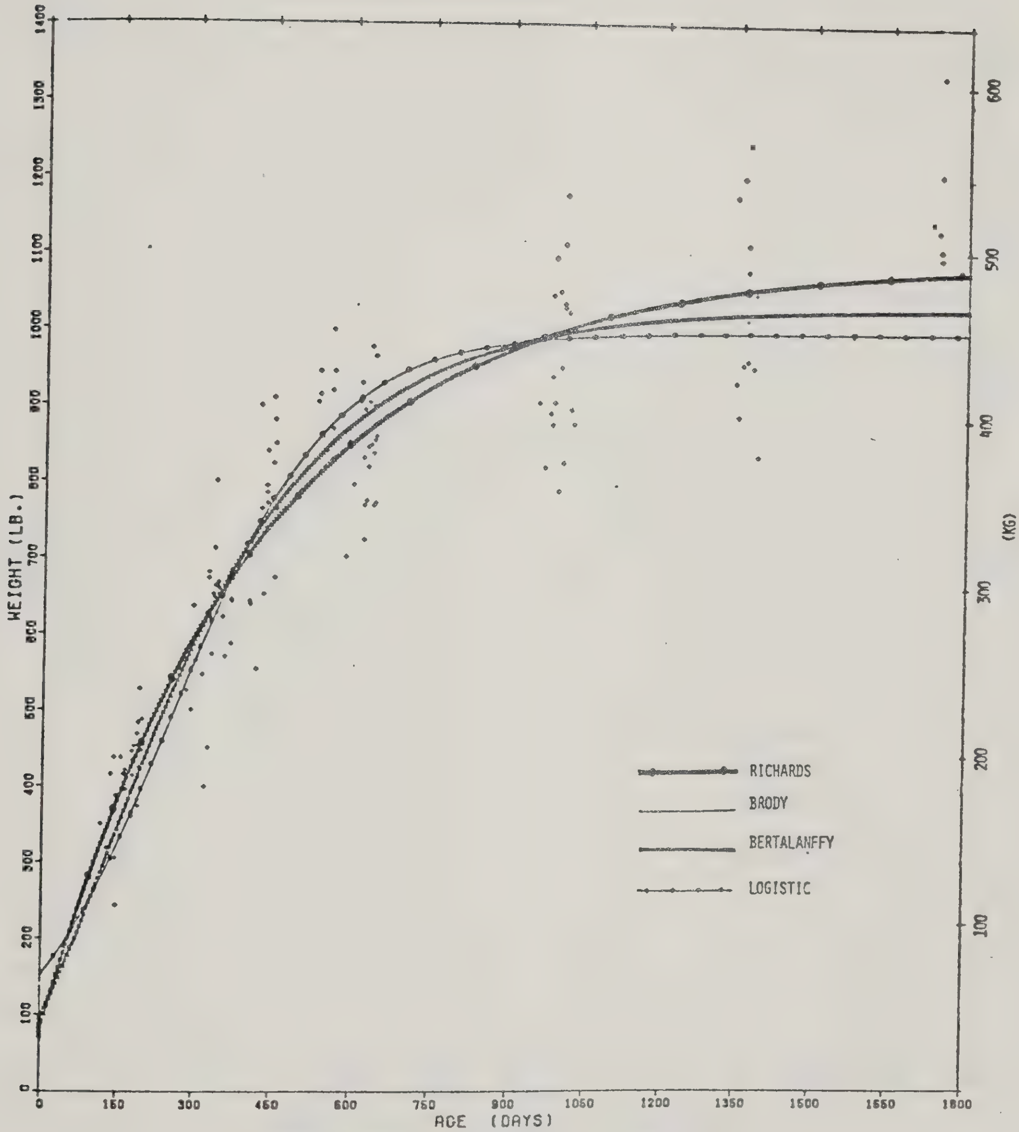

Fig. 5. GROWTH CURVES. WITH DATA FOR BREED BR 50% LD 50%

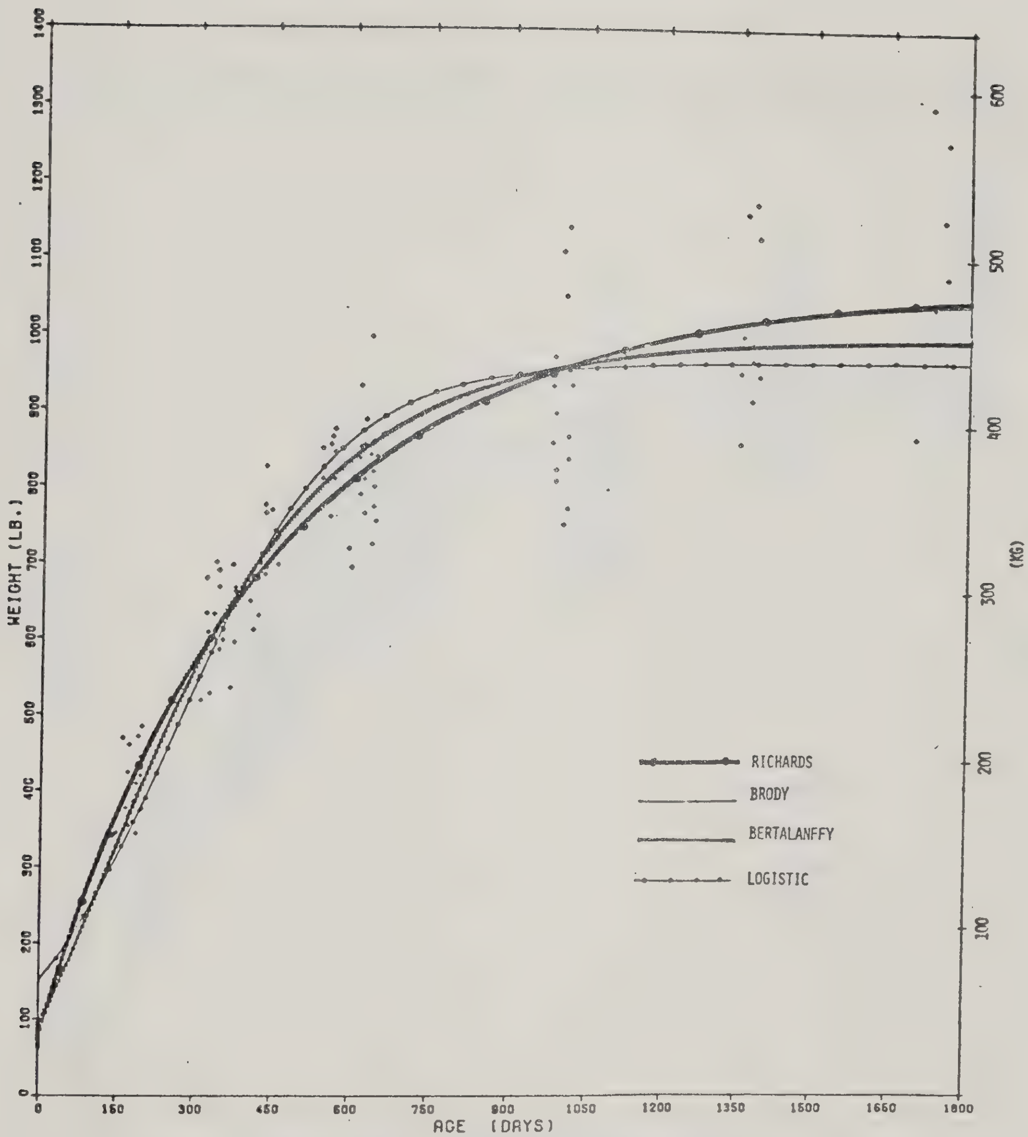

Fig. 6. GROWTH CURVES. WITH DATA FOR BREED LB 75%

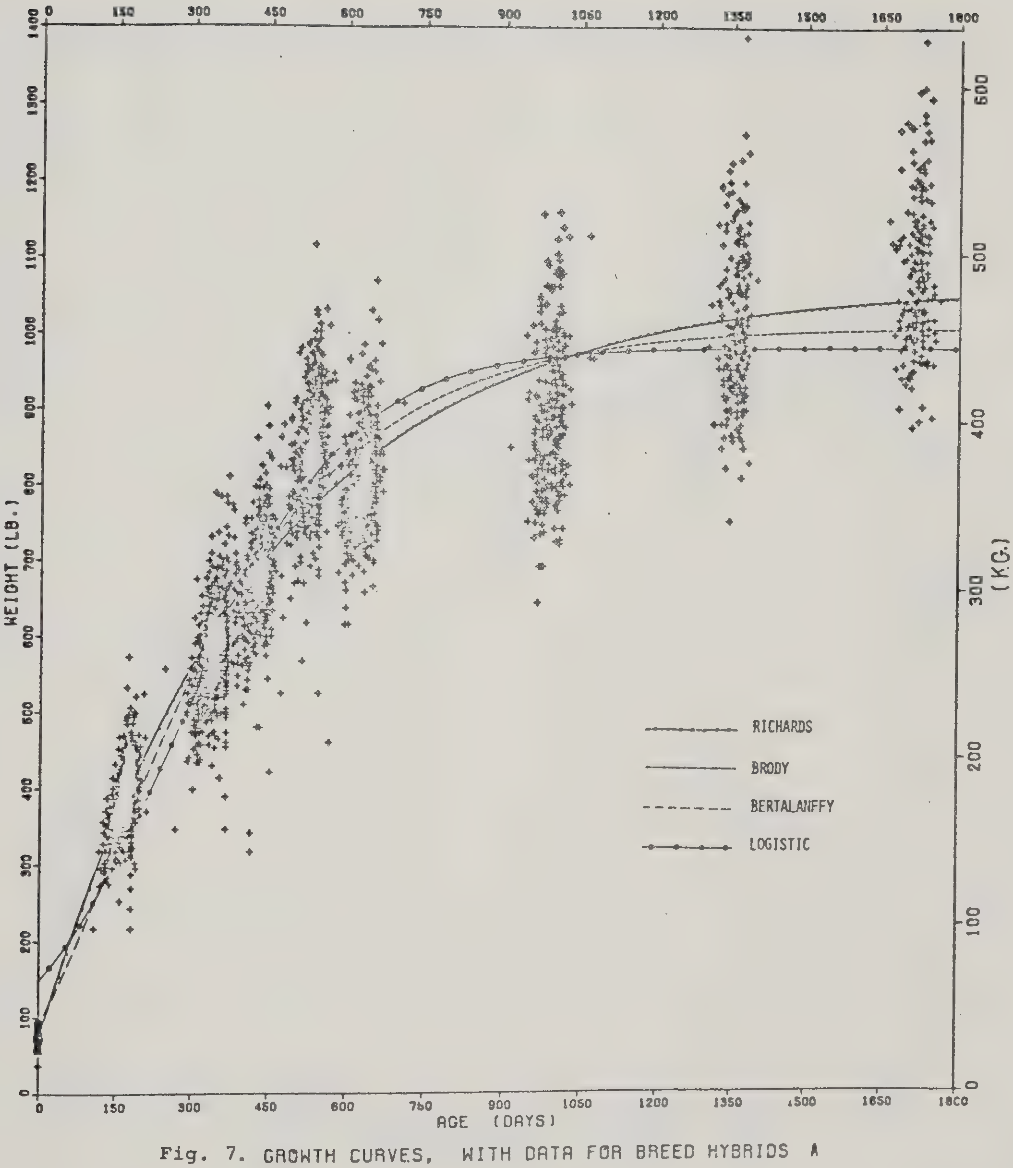

Fig. 7. GROWTH CURVES, WITH DATA FOR BREED HYBRIDS A

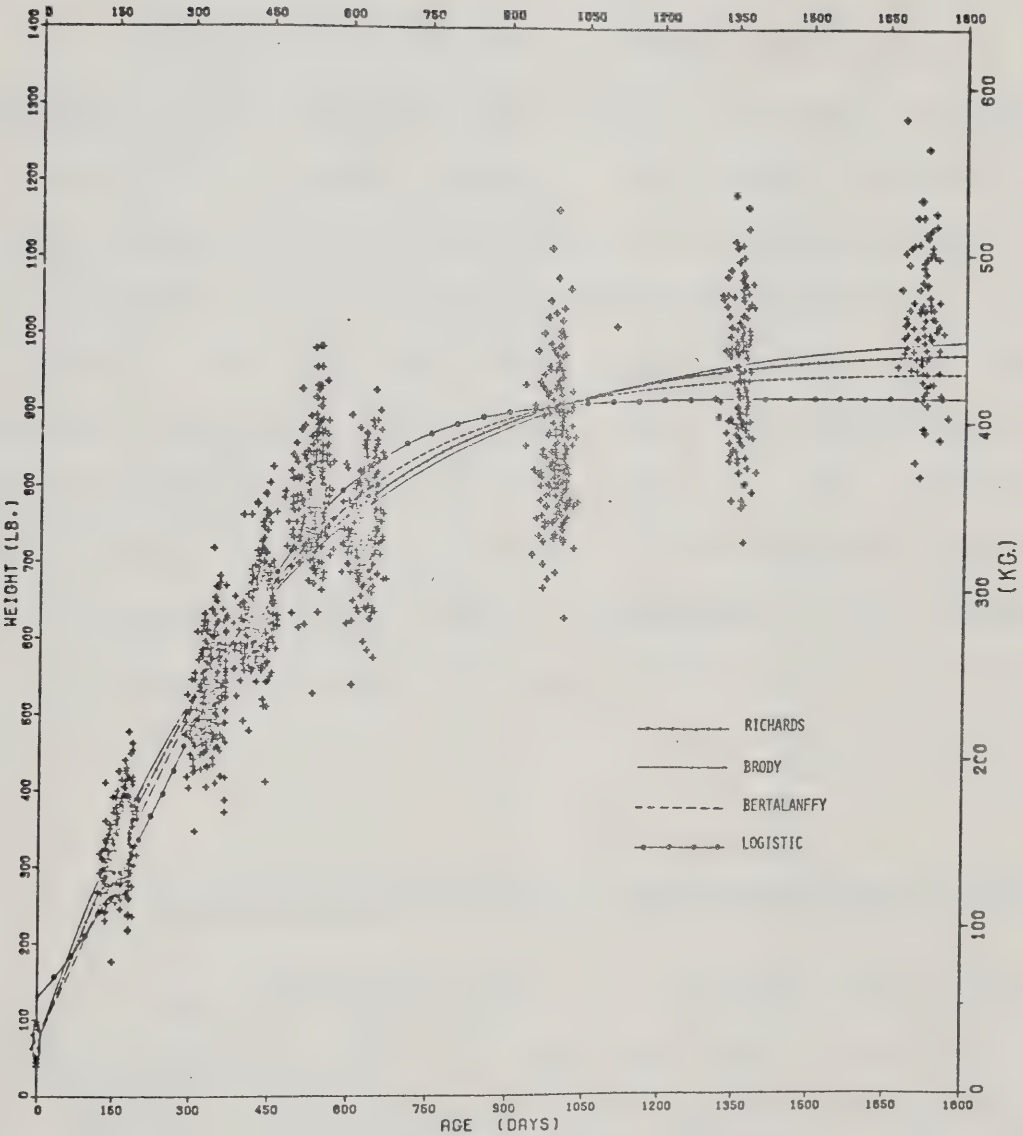

Fig. 8. GROWTH CURVES, WITH DATA FOR BREED HEREFORDS A

6.3 Analysis of overall fit

6.3.1 Parameter fit

The proportions of the total variance accounted for by regression in each function and residual variances are shown in Table 12 by breed group. The values reported are therefore estimates of the accuracy of the iterative fit of the parameters and reflect the overall comparative fit of the models. In all data sets the Richards and Brody functions provided better fits than the Bertalanffy and Logistic functions. The Richards, being a four parameter model should account for more of the variation than the three parameter models. However comparisons of the Richards with the Brody model show no improvement in fit in data sets.

6.3.2 Analysis of the overall fit within breed groups

The mean prediction estimates, residual mean squares, standard deviations, over all ages are shown in Table 13 for the unadjusted and adjusted data from the Hybrid and Hereford lines and the four XB groups (100% BR, 75% BR, 50% BR 50% LD and 75% LB). The growth functions applied to all of the data sets tended to overestimate weight from birth to 56 months of age as all mean prediction error

Table 12. Values of R^2 and residual variances by function and breed group

Breed Group	Function	% R^2	Residual Variance
Hybrid [1]	Richards	93.9	4013916.0
	Brody	93.6	4179393.0
	Bertalanffy	92.6	4851124.0
	Logistic	90.6	6186205.0
Hybrid [2]	Richards	93.4	4096481.0
	Brody	93.4	4096726.0
	Bertalanffy	93.0	4355497.0
	Logistic	91.6	5272479.0
Hereford [1]	Richards	94.8	2030715.0
	Brody	94.8	2045383.0
	Bertalanffy	94.1	2319372.0
	Logistic	92.2	3046321.0
Hereford [2]	Richards	94.2	2178768.0
	Brody	94.1	2209446.0
	Bertalanffy	94.1	2238985.0
	Logistic	92.8	2706326.0
100% BR	Richards	94.8	499724.0
	Brody	94.8	499927.0
	Bertalanffy	94.4	534475.0
	Logistic	92.9	682313.0
75% BR	Richards	93.6	946571.0
	Brody	93.6	950031.0
	Bertalanffy	93.4	984083.0
	Logistic	92.0	1191425.0
50% BR 50% LD	Richards	94.0	509425.0
	Brody	94.0	509454.0
	Bertalanffy	93.6	542974.0
	Logistic	92.1	674866.0
75% LB	Richards	94.4	338389.0
	Brody	94.4	338826.0
	Bertalanffy	93.8	372223.0
	Logistic	92.0	482848.0

[1]Unadjusted weight data
[2]Adjusted weight data

Table 13. Mean prediction error estimates, residual mean squares, and standard deviations by function and breed group

Breed Group	Function	Mean Prediction error (%)	Residual Mean Square	Standard Deviation (%)
Hybrid [1]	Richards	-1.287a	145.083	12.363
	Brody	-3.208b	150.950	14.094
	Bertalanffy	-5.484c	161.832	19.893
	Logistic	-17.333d	214.117	47.982
Hereford [1]	Richards	-1.224a	158.532	12.845
	Brody	-1.940a	159.385	12.832
	Bertalanffy	-4.125b	165.564	16.965
	Logistic	-15.670c	237.675	42.499
Hybrid [2]	Richards	-1.287a	144.091	12.341
	Brody	-1.211a	143.958	12.342
	Bertalanffy	-3.817b	150.991	15.915
	Logistic	-14.320c	205.126	40.312
Hereford [2]	Richards	-1.382b	141.418	12.121
	Brody	-0.149a	140.263	13.027
	Bertalanffy	-2.658c	145.077	13.501
	Logistic	-12.045d	193.612	34.051
100% BR	Richards	-0.762a	106.436	10.655
	Brody	-0.618a	106.088	10.727
	Bertalanffy	-2.784b	112.596	12.840
	Logistic	-13.086c	159.686	35.343
75% BR	Richards	-1.427ab	189.946	13.946
	Brody	-0.917a	186.394	14.137
	Bertalanffy	-3.209b	204.796	15.765
	Logistic	-13.265c	308.801	36.513
50% BR 50% LD	Richards	-1.143a	146.621	12.173
	Brody	-1.179a	146.732	12.199
	Bertalanffy	-3.298b	144.585	14.232
	Logistic	-13.706c	165.610	36.178
75% LB	Richards	-0.800a	106.057	10.469
	Brody	-1.058a	106.713	10.397
	Bertalanffy	-3.306a	113.706	13.446
	Logistic	-14.112b	163.091	37.906

[1]Unadjusted weight data
[2]Adjusted weight data.
Mean prediction error estimates with the different alphabetic letters within a breed are significant P<0.05

estimates were negative. The results based on the R^2 values are similar to the results using a mean prediction error estimate when the 3 parameter models were compared.

Based on the magnitude of the residual mean squares the Richards growth function provided the best fit to the unadjusted weight data from the Hybrid and Hereford lines, 50% BR 50% LD and 75% LB breed groups; while the Brody function offered the best overall fit to the adjusted weight data from the Hybrid and Hereford lines, the 100% BR and 75% BR breed groups. The Bertalanffy and the Logistic function were consistently poor in predicting weights over the entire growth curve.

Brown et al. (1976) used a similar approach to evaluate the fit of five growth models to beef cattle data from two locations. According to their results the Brody function showed a low residual variance and hence a better fit to one set of data while the Richards provided a better fit to the other set of data. The Logistic function showed the highest residual mean square and hence the poorest fit in both locations. The results of the present analysis show that the Richards and Brody functions had a better fit than the Bertalanffy and Logistic functions.

Comparing the overall fit between functions within breed groups, a lower residual mean square was always

associated with a lower mean prediction error. The Richards function had the lowest mean prediction error when applied to the unadjusted data from the Hybrid and Hereford lines and this value was significantly different for the Hybrids but not for the Herefords. The Bertalanffy and Logistic functions gave poorer fits.

In the adjusted data from the Hybrid line low mean prediction error estimates were obtained for weights based on the Brody function followed by the Richards, Bertalanffy and Logistic functions. Thus, in the adjusted data the Brody function provided the best fit over the entire growth curve although, the mean prediction error estimates were not significantly different from the mean prediction error estimates based on the Richards function. In the adjusted weight data from the Hereford line, the Brody function provided the lowest prediction error which was significantly different from the prediction error estimate based on the Richards function. The Bertalanffy and Logistic functions provided a poorer fit and the error estimates were significantly higher compared to the Richards and Brody functions.

In the 100% BR breed group the Brody function provided a good fit having a small mean prediction error although the error estimates based on the Richards was not significantly different. Similar trends were established in the other

breed groups. In general the fit of the Brody and Richards functions were similar and always significantly different from the Logistic. The mean prediction error based on the Bertalanffy was similar to the Richards in the 75% BR group and similar to the Richards and Brody in the 75% LB breed group.

The value of an empirical technique in describing growth data depends on the accuracy with which each data point is predicted. Brown et al (1976) stated that the usual test of the goodness of fit may be inaccurate because of the correlated errors among longtitudinal data points. Thus, the authors claim that in their study the evaluation of fit was subjective, in which the observed and predicted weights at each weight-age point were compared. The similarity between the methods using residual mean squares and standardised mean prediction errors in evaluating the fit of growth functions justifies the latter as a suitable procedure. The technique of using prediction error estimates in growth curve analysis has not been previously reported in the literature.

6.3.3 Comparison of overall fit between unadjusted and adjusted data within function and breed

Table 14 shows the overall mean prediction error

Table 14. Comparison of unadjusted and adjusted data within function and breed group

Breed Group	Function	Mean Prediction Error (%) unadj.	Mean Prediction Error (%) Adj.	Difference
Hybrid		n=1409	n=3137	
	Richards	-1.287	-1.287	0.0
	Brody	-3.208	-1.211	-1.997**
	Bertalanffy	-5.484	-3.817	-1.667**
	Logistic	-17.333	-14.320	-3.013**
Hereford		n=951	n=2159	
	Richards	-1.224	-1.382	0.158
	Brody	-1.940	-0.149	-1.741**
	Bertalanffy	-4.125	-2.658	-1.467*
	Logistic	-15.670	-12.045	-3.625**

*P<0.05
**P<0.01

estimates based on each growth function for the unadjusted and adjusted weight data, and the difference between estimates within function and breed group. The overall mean prediction error estimates based on the Richards function were not significantly different between the unadjusted and adjusted data in the Hybrid and Hereford breed groups. The Richards function further fitted the unadjusted and adjusted data with the same mean prediction error.

The fit of the Brody, Bertalanffy and Logistic functions was significantly improved by fitting adjusted weights in both breed groups.

The residual mean squares from a one way anova for the unadjusted and adjusted weight data are shown in Table 15 by function and breed group. Examination of the residual mean squares in both breed groups suggests that adjusting for year and age of dam effects reduced the residual variance within each function.

In fitting growth models to adjusted weight data one of two things could happen. Firstly, the mean prediction error estimates could be reduced and secondly, the variation in the data sets could be reduced. In all but the Richards function fitted to the Hybrid and Hereford data adjusted for year and age of dam, the mean prediction error estimates and the residual variance were reduced suggesting an improved

Table 15. Residual mean squares for the unadjusted and adjusted data by function and breed group

		Residual mean squares			
Breed	Data	Richards	Brody	Bertalanffy	Logistic
Hybrid	Unadj.	145.08	150.95	161.83	214.12
	Adj.	144.09	143.96	150.99	205.13
Hereford	Unadj.	158.53	159.39	165.56	237.68
	Adj.	141.42	140.26	145.00	193.61

fit of the models. Although the overall fit of the four models was improved by adjusting the data the overall mean prediction error estimates based on the Logistic function being high, adjusting the data had its greatest practical implications in improving the fit of the Brody and possibly the Bertalanffy functions.

6.3.4 Analysis of the overall consistency of fit between breed groups

Table 16 shows the overall mean prediction error estimates based on the four growth functions and the differences between estimates compared between breeds and within each type of data.

The Richards function provided the most consistent overall fit to the two breed groups within each data type as none of the breed differences were significant, the mean prediction error estimates being small and similar. The Brody, Bertalanffy and Logistic functions were less consistent as mean prediction error estimates between breed groups were different. Although the difference between the mean prediction error estimates based on the Bertalanffy and Logistic functions fitted to the unadjusted Hybrid and Hereford data were consistent between breeds, they were large.

Table 16. Overall mean prediction error estimates and differences between breed groups

Type of Data	Breed Group	Mean Prediction Error (%)							
		Richards	Difference	Brody	Difference	Bertalanffy	Difference	Logistic	Difference
Unadjusted	Hybrid	-1.287	-0.063	-3.208	-1.268**	-5.484	-1.359	-17.333	-1.663
	Hereford	-1.224		-1.940		-4.125		-15.670	
Adjusted	Hybrid	-1.287	0.095	-1.211	-1.062*	-3.817	-1.159**	-14.320	-2.275**
	Hereford	-1.382		-0.149		-2.658		-12.045	

*P<0.05
**P<0.01

Table 17. Mean prediction error estimates by function in the XB groups

	Mean Prediction Error (%)			
Breed Group	Richards	Brody	Bertalanffy	Logistic
100% BR	-0.762a	-0.618a	-2.784a	-13.086a
75% BR	-1.427a	-0.917a	-3.209a	-13.265a
50% BR 50% LD	-1.143a	-1.179a	-3.298a	-13.706a
75% LB	-0.800a	-1.058a	-3.306a	-14.112a

a-None of the mean prediction errors in columns were significantly different $P<0.05$

Table 17 shows the overall mean prediction error estimated by each function in the XB groups. All mean prediction error estimates were similar within function and between breeds. However, only the estimates based on the Richards and Brody were small as well as consistent.

6.3.5 Conclusions

The Richards and Brody functions provided the best overall fit to all of the data sets. Bertalanffy and Logistic functions in general did not provide a good fit.

Adjusting the data for year and age of dam reduced the residual variance in the two breed groups while significant reduction of the mean prediction error estimates were observed in the estimates based on the Brody, Bertalanffy and Logistic functions.

The Richards function provided the most consistent estimate of error between breeds and was thus best suited for parameter comparisons.

6.4 Parameter estimates of growth functions

The values of the fitted parameters (A), (B), (k) and (M) and standard deviations computed by each function in each breed group are shown in Table 18. Due to the variable

Table 18. Estimates of fitted parameters by function and breed group

Breed Group	Function	Asymptote (A) kg	(B)	Maturing Rate (k) %	(M)
Hybrid [1]	Richards	521.61	0.984±.004	0.126±.009	0.663±.029
	Brody	484.00	0.922±.005	0.205±.004	-
	Bertalanffy	455.23	0.535±.009	0.340±.005	-
	Logistic	442.39	4.989±.017	0.554±.011	-
Hybrid [2]	Richards	481.64	0.927±.001	0.232±.001	1.019±.042
	Brody	482.50	0.932±.003	0.283±.002	-
	Bertalanffy	456.68	0.551±.006	0.368±.003	-
	Logistic	444.33	5.584±.123	0.615±.007	-
Hereford [1]	Richards	476.16	0.960±.009	0.161±.010	0.846±.049
	Brody	463.77	0.928±.005	0.191±.004	-
	Bertalanffy	433.03	0.545±.009	0.322±.005	-
	Logistic	419.64	5.340±.201	0.546±.012	-
Hereford [2]	Richards	444.86	0.857±.002	0.271±.009	1.359±.081
	Brody	456.60	0.938±.003	0.220±.003	-
	Bertalanffy	430.41	0.561±.006	0.359±.003	-
	Logistic	414.65	0.064±.153	0.628±.008	-
100% BR	Richards	463.18	0.919±.037	0.264±.029	1.047±.015
	Brody	465.09	0.920±.011	0.254±.011	-
	Bertalanffy	441.07	0.552±.020	0.411±.012	-
	Logistic	425.81	5.719±.470	0.708±.033	-
75% BR	Richards	452.01	0.893±.042	0.277±.027	1.173±.171
	Brody	458.91	0.932±.009	0.246±.009	-
	Bertalanffy	432.40	0.553±.017	0.404±.001	-
	Logistic	415.87	5.838±.400	0.705±.002	-
50% BR 50% LD	Richards	494.69	0.923±.043	0.243±.035	1.019±.018
	Brody	495.60	0.928±.013	0.239±.012	-
	Bertalanffy	467.31	0.547±.023	0.391±.014	-
	Logistic	452.47	5.544±.510	0.663±.035	-
75% LB	Richards	482.79	0.943±.036	0.217±.035	0.934±.160
	Brody	478.66	0.926±.014	0.233±.013	-
	Bertalanffy	451.56	0.545±.026	0.351±.015	-
	Logistic	437.71	5.378±.570	0.636±.039	-

[1]Unadjusted weight data
[2]Adjusted weight data

number of animals in the sets of data, the parameter estimates of the Hybrid and Hereford breed groups will be discussed separately from the parameter estimates of the four XB groups.

6.4.1 Asymptotes (A)

The mean observed and predicted adult weight (56 months) and the asymptotes estimated by each growth function for each data set and breed group are shown in Table 19.

In the Hybrid and Hereford populations with the unadjusted weight data, the Richards function estimated the highest asymptote followed by the Brody, Bertalanffy and Logistic functions. However, in the adjusted data the asymptotes fitted by the Brody function were slightly higher than the Richards. The asymptotes fitted by the Brody, Bertalanffy and Logistic functions were similar in both data sets within breed and function while the asymptotes fitted by the Richards function were higher in the unadjusted data sets of both breed groups. Furthermore, in the adjusted weight data, the asymptotes fitted by the Richards function were lower than the observed adult weights, while the reverse was true in the unadjusted data sets.

In the Hybrid breed group using unadjusted data adult weight was underestimated by 9.16 kg and 19.72 kg based on

Table 19. Mean observed, predicted adult weights and asymptotes by function and breed group

Breed Group	Function	Unadjusted			Adjusted		
		Observed Adult wt (kg) 56 month	Predicted Adult wt (kg) 56 month	A (kg)	Observed Adult wt (kg) 56 month	Predicted Adult wt (kg) 56 month	A (kg)
Hybrid	Richards	490.39	481.23	521.61	493.75	474.63	481.64
	Brody		470.67	484.00		475.09	482.50
	Bertalanffy		453.97	455.23		456.86	456.68
	Logistic		442.25	442.39		445.80	444.33
Hereford	Richards	459.95	457.78	476.16	461.18	438.17	444.86
	Brody		447.64	463.77		444.99	456.60
	Bertalanffy		430.22	433.03		427.15	430.41
	Logistic		419.45	419.64		412.84	414.65

the Richards and Brody functions respectively while adult weight was underestimated by 19.12 kg and 18.66 kg based on the same functions using the adjusted data. Similarly among the Herefords the differences between the observed and predicted adult weight based on the Richards was greater in the adjusted data which reflected the lower fitted asymptotes in these data.

Although all weights were adjusted, adjusting the weights at 32 months, 44 months and 56 months of age for the year effects in the Hybrid data was more critical in determining the asymptote and decreased the mean weight at each of these ages (Table 10). Similarly, in the Hereford breed group mean 32 month and 44 month weight was decreased and 56 month weight increased (Table 11). The general reduction of mean body weights during later ages by adjusting the data would have accounted for the lower asymptotes and mean predicted adult weights in the Hybrid breed group. The effects of adjusting were however less pronounced in the Hereford breed group. In general predicted adult weight was underestimated to a greater degree by adjusting the data, which reduced the asymptotic weights fitted by the Richards model in particular. The asymptotes based on the Brody, Bertalanffy and Logistic models were relatively insensitive to the changes in weight due to adjusting.

Brown et al. (1976) in a study comparing the relative efficiency of 5 non linear models in describing growth of Herefords fitted asymptotes of 505 kg, 508 kg, 488 kg and 481 kg using the Richards, Brody, Bertalanffy and Logistic[1] functions respectively, compared with fitted asymptotes of 476 kg, 464 kg, 433 kg and 420 kg in the present analysis using unadjusted weights based on the Richards, Brody, Bertalanffy and Logistic functions. The 30-60 kg difference between asymptotes of the two studies could be due to the choice of weights and the time at which weights were recorded in relation to season or to time differences in environment.

In every set of data under study the Bertalanffy and Logistic functions fitted asymptotes that were below the observed adult weight and almost equal to the predicted adult weight. A rapid convergence pattern and underestimation of the asymptote is therefore characteristic of the two functions. When the estimated shape parameter (M) of the Richards function was close to 1 (Table 18) the fit and consequently the asymptotes computed by the Richards were almost identical to the Brody, as the computational formulae of the two functions were identical when M=1.

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[1]A modified form of the Logistic function with a variable point of inflection was used in this study

Table 20 shows the mean observed and predicted adult weights and fitted asymptotes by function for the four XB groups. In the four XB groups with the exception of the 75% LB breed group the Brody function fitted the highest asymptote. The Richards function estimated a high asymptote to the 75% LB group. However, the asymptotes fitted by the Richards and Brody functions were similar between groups and differences never exceeded 7 kg. Furthermore, in all XB groups the fitted asymptotes were lower than the mean observed adult weight and in every instance adult weight was underestimated. The Logistic was similar to the Bertalanffy in fitting low asymptotes which closely approximated the mean predicted adult weight. Due to the fewer number of observations available at 56 months of age and the variation in the available observations the fitted asymptotes and predicted adult weights may not adequately characterize each breed group.

6.4.2 Maturing rates (k)

The parameter (k) is a general maturing rate parameter calculated over the entire growth curve period.

Comparing the (k) values from the Richards function (Table 18) using the unadjusted weight data there was a 28% difference in maturing rates, Herefords being earlier

Table 20. Mean observed, predicted adult weights and asymptotes by function for the XB groups

Breed Group	Function	Mean Observed Adult wt (kg) 56 month	Mean Predicted Adult wt (kg) 56 month	A (kg)
100% BR	Richards	482.92	458.49	463.18
	Brody		459.75	465.09
	Bertalanffy		440.46	441.07
	Logistic		425.83	425.81
75% BR	Richards	486.39	448.05	452.01
	Brody		452.76	458.91
	Bertalanffy		431.71	432.40
	Logistic		415.85	415.87
50% BR 50% LD	Richards	530.81	487.94	494.69
	Brody		488.50	495.60
	Bertalanffy		466.47	467.31
	Logistic		452.46	452.47
75% LB	Richards	495.71	473.16	482.79
	Brody		470.88	478.66
	Bertalanffy		450.54	451.56
	Logistic		437.68	437.71

maturing than Hybrids, while a 17% difference was observed with the adjusted data. On the other hand based on the (k) values derived from the Brody function in the unadjusted weight data the Herefords showed a 7% lower maturing rate. Brown et al (1976) reported similar results while comparing the maturing rates derived by the Brody and Richards functions among Jerseys and Herefords. Based on the Richards function the Herefords matured later than the Jersey while based on the Brody function the Jerseys matured later. However no attempt was made to explain this difference.

Comparisons of maturing rates based on the growth models were reported between breed groups (Brown et al, 1976) and between sexes within breeds (Brown et al, 1972a). The values of the maturing rate parameter (k) computed on each model in the present study were comparable with the results in the literature.

The values of (k) based on the Richards and Logistic functions differed widely in each set of data and similar observations were reported by Brown et al (1976) and Timon and Eisen (1969). In the study of Timon and Eisen (1969) heritability estimates for the parameter (k) based on the Richards and Logistic functions were 0.30 and 0.76 respectively. The genetic correlation between the parameter (k) calculated from the two functions was 0.0. The authors

therefore suggested that the two functions may be estimating different parameters. In contrast, the correlations between functions of the asymptotes (A) were highly positive and approached unity (Timon and Eisen, 1969).

The differences between the (k) values of the unadjusted and adjusted data based on the Richards was in part due to the lower asymptotes fitted when the data were adjusted. The differences between unadjusted and adjusted (k) values based on the Brody function were less pronounced between data sets within a breed group because the asymptotes were reduced to a lesser degree by adjusting the data.

The Richards and Brody functions were consistent in fitting the XB groups with small and uniform mean prediction error estimates and were thus ideal for parameter comparisons (Table 17). However the Richards function provided a poorer fit to the 75% BR group. Comparing the values of (k), among the XB groups (Table 18) the lowest values of (k) were observed in the 75% LB breed group, suggesting that the 75% LB dams matured slower than the other three breed groups. British breeds of cattle, namely Angus and Hereford are early maturing (Berg and Butterfield, 1976) and in this analysis an increase in the proportion of large beef blood would be expected to reduce maturing rates. Based on the Brody function the values of (k) were lower for

the 75% BR group compared to the 100% BR group. It is therefore indicative that the 75% BR dams matured later than the 100% BR dams. The maturing rates computed by all growth functions for the 50% BR 50% LD breed group were lower than the maturing rates of the 75% BR group suggesting that the British/Dairy crosses (50% BR 50% LD) are later maturing.

In general, the 75% LB breed group showed a late maturing pattern followed by the 50% BR 50% LD, 75% BR and 100% BR groups. The maturing rates in the four XB groups appeared to be directly proportional to the amount of British beef blood. However, because of the small size of sample analysed the results cannot be considered as being absolutely conclusive.

6.4.3 Inflection parameters (Y*), (t*)

The weight at point of inflection (Y*) and the age at which inflection occurs are shown in Table 21 by function and breed group for the unadjusted and adjusted data. As the Logistic and Bertalanffy functions have inflection weights that are fixed (Table 5), there is very little variation in the estimates of (Y*) and (t*). The Richards which has a variable inflection point allows variation in the estimates. Based on the Richards function the mean weights at point of inflection (unadjusted and adjusted)

Table 21. Inflection parameters by function and breed group

		Weight at inflection (Y^*) kg				Time of inflection (t^*) days		
Breed Group	Data Type	Richards	Brody	Bertalanffy	Logistic	Richards	Bertalanffy	Logistic
Hybrid	Unadjusted	154.00	177.16	134.75	222.32	n.e.	139	290
	Adjusted	178.86	176.60	135.18	222.17	n.e.	137	280
Hereford	Unadjusted	160.75	169.74	128.18	209.82	n.e.	153	306
	Adjusted	189.29	167.12	127.40	207.33	n.e.	145	287

Weight at inflection for the Brody function was calculated as $M + 1$.

n.e. = not estimable

were 171 kg and 182 kg for the Hybrid and Hereford groups. Fitzhugh (1976) states that as the growth curve is essentially linear at inflection the estimated point of inflection is influenced more by the type of function used rather than the animals genotype. In cattle the time of inflection occurs at a point between 6 to 18 months of age (Fitzhugh, 1976). The time of inflection for the Richards function could not be determined in this study.

6.4.4 Conclusions

The Brody and Richards function fitted larger asymptotes in all breed groups compared to the Bertalanffy and Logistic functions.

All growth functions fitted higher asymptotes to the Hybrid data compared to the Herefords illustrating that the Hybrids achieve higher mature weights.

In the adjusted data due to a general reduction of body weight during the later ages, the asymptotes fitted by the Richards function was markedly lower in both breed groups while the Brody, Bertalanffy and Logistic functions were relatively insensitive to such changes and fitted similar asymptotes to the unadjusted and adjusted Hybrid and Hereford data.

The Bertalanffy and Logistic functions converged sharply at the asymptote therefore resulting in lower asymptotes. The predicted adult weight and the asymptotes were markedly similar within function. The asymptotes fitted by the four growth functions for the Herefords were comparable with reports in the literature.

Based on the Richards function which offered a consistent fit to all of the data the Herefords were recognised as being early maturing compared to the Hybrids. The (k) values fitted by the Richards and Logistic functions within breed and data set were different suggesting that the two models may be fitting parameters of different biological significance.

The differences in the (k) values fitted by the Richards and Brody functions between the unadjusted and adjusted data within breeds are attributed to the differences in the fitted asymptotes.

Based on a limited number of observations the 75% LB breed group was later maturing compared to the other XB groups. The maturing rates were proportional to the amount of British beef blood present in the four XB groups.

6.5 Analysis of Hybrid data

6.5.1 Analysis of the goodness of fit of each growth function applied to each age

Table 22 shows the mean prediction error estimates, standard errors, and differences between unadjusted and adjusted mean prediction error estimates by function at each age for the Hybrid breed group. The minima and maxima for the % mean prediction error by function and age for the Hybrid data sets are shown in Appendix Table 1.

Birth: In the unadjusted Hybrid weight data the Richards function showed the smallest mean prediction error 0.67% for birth weight followed by the Brody, Bertalanffy and Logistic functions. The 3 latter functions overestimated birth weight; the Logistic function overestimating weight by 126.6%. The mean prediction error estimates computed by the Richards function was significantly less than from the other three. The Bertalanffy and Logistic functions predicted minima and maxima which were both negative and thus reflected their poor performance in predicting birth weight (Appendix Table 1).

In the adjusted Hybrid data the Brody function provided the best fit to the weight at birth followed by the Richards model. The mean prediction errors calculated on the Brody

Table 22. Mean prediction error estimates and standard errors (Se) for unadjusted and adjusted Hybrid data and differences

Age	Number of Animals	Function	Mean Prediction Error (%) [1]	Se. (%) [1]	Mean Prediction Error (%) [2]	Se. (%) [2]	Difference
Birth	203 [1]	Richards	0.673a	0.927	-0.633a	0.590	1.306
		Brody	-18.238b	1.104	0.118a	0.585	-18.356**
	454 [2]	Bertalanffy	-40.000c	1.307	-25.285b	0.734	-14.715**
		Logistic	-126.590d	2.115	-104.438c	1.198	-22.152**
Weaning	203	Richards	-5.115b	0.967	-0.327a	0.617	-4.788**
		Brody	2.460a	0.888	-0.645a	0.619	3.105**
	439	Bertalanffy	10.500c	0.814	9.206b	0.566	1.294
		Logistic	12.762d	0.800	14.755c	0.527	-1.993*
Yearling	196	Richards	-0.240a	0.623	-2.861ab	0.411	2.621**
		Brody	-0.209a	0.615	-2.855ab	0.411	2.652**
	488	Bertalanffy	-0.943a	0.615	-3.304b	0.399	2.361**
		Logistic	1.179b	0.603	-1.732a	0.383	2.911**
20 months	177	Richards	2.000a	0.641	2.055b	0.450	-0.055
		Brody	-0.456b	0.657	2.135b	0.450	-2.591**
	290	Bertalanffy	-4.086c	0.680	-0.603a	0.464	-3.483**
		Logistic	-7.262d	0.700	-3.433c	0.483	-3.829**
32 months	158	Richards	-6.950a	1.065	-8.394a	0.713	1.444
		Brody	-8.843ab	1.064	-8.352a	0.713	-0.491
	269	Bertalanffy	-10.164bc	1.097	-8.774a	0.718	-1.390
		Logistic	-11.571c	1.112	-9.151a	0.723	-2.420
44 months	142	Richards	-1.355a	0.892	-1.488b	0.670	0.133
		Brody	-1.088a	0.890	-1.526b	0.671	0.438
	223	Bertalanffy	0.731ab	0.875	0.783a	0.656	-0.052
		Logistic	1.706b	0.866	2.499c	0.645	-0.793
56 months adult	128	Richards	0.936a	0.845	3.025a	0.664	-2.089*
		Brody	3.108a	0.827	2.932a	0.665	0.176
	185	Bertalanffy	6.731b	0.797	6.667b	0.640	0.064
		Logistic	8.488b	2.783	8.933c	0.624	-0.445

[1]Unadjusted
[2]Adjusted
a,b,c,d - Mean prediction error estimates with different alphabetic letters within an age are significant $P<0.05$
*$P<0.05$
**$P<0.01$

and Richards functions were not significantly different although they were significantly smaller than those from the Bertalanffy and Logistic functions.

In general, the Richards function was consistently good in describing birth weight in the two sets of Hybrid data and the Brody was equally good for the adjusted data. The Bertalanffy and Logistic functions were unsatisfactory in predicting birth weight as they were associated with large mean prediction errors.

Weaning: At weaning the Brody function provided a good fit in both sets of data. The Brody function provided an error that was significantly less than the Richards in the unadjusted Hybrid data but not significantly different in the adjusted data. In the unadjusted Hybrid data the Richards function tended to overestimate weaning weight while the Brody, Bertalanffy and Logistic functions underestimated weaning weight. However, weaning weight was underestimated by only the Bertalanffy and Logistic functions in the adjusted data. The Bertalanffy and Logistic growth functions provided poor estimates of weaning weight as the mean prediction errors were significantly larger than those computed on the Richards and Brody functions in both sets of data.

Yearling: At the yearling weight, all mean prediction

error estimates computed by each growth function applied to the unadjusted Hybrid data set were small. A comparison of mean prediction error estimates applied to the same population showed the mean prediction error estimates for the Richards, Brody and Bertalanffy functions were similar, and these were significantly different from the error estimated by the Logistic function. In the adjusted Hybrid data, the magnitude of error was similar although the mean prediction error computed by the Bertalanffy function in the adjusted Hybrid data was significantly higher than the Logistic. Thus, considering both the unadjusted and adjusted data the four growth functions gave a satisfactory prediction of yearling weight; the Brody function ranking the best among the unadjusted yearling weights and the Logistic ranking the best among the adjusted yearling weights.

20 months: The weight at 20 months was best predicted by the Brody function with less than -0.5% error in the unadjusted data and by the Bertalanffy with less than a 0.61% mean prediction error in the adjusted data. The mean prediction error estimated by the Brody function was significantly lower than the mean prediction errors estimated by the other growth functions in the unadjusted Hybrid data while the mean prediction errors based on the Bertalanffy function was significantly lower than the mean

prediction errors based on the other growth functions in the adjusted data. The mean prediction errors based on the Logistic function were consistently larger in all of the data sets.

<u>32 months</u>: At 32 months there was a general overestimation of weight by all four growth functions in both sets of data. The mean prediction error estimates were also higher in all functions compared to the mean prediction error estimates at yearling and 20 months. In the unadjusted data the Richards function provided a better fit although its mean prediction error was not significantly different from that of the Brody function. Similarly, no significance was established between the mean prediction errors estimated by the Brody and Bertalanffy functions and the Bertalanffy and Logistic functions. In the adjusted Hybrid data the Brody function provided a relatively low prediction error although the error estimates computed by the other functions were not significantly different from the Brody function.

The standard errors of the mean prediction error estimates at 32 months were higher in all sets of Hybrid data than standard error estimates during all intermediate ages. During this time, cows usually lost weight due to an imposed temporary winter stress and were in a state of negative growth. Furthermore, as animals had passed the

point of inflection their growth rates were decreasing. A combination of these factors can cause significant deviations from a normal growth pattern and this effect is recognised when growth equations are fitted to these types of data. As each growth curve assumes a characteristic growth pattern it is not sensitive in reacting to sudden fluctuations resulting in a decrease in weight and thus will overestimate weight at such stages, as illustrated, at 32 months of age. In general, all functions gave poor estimations of weight at this age with mean prediction errors ranging from 7% to 11.6%.

44 months: At 44 months of age the Bertalanffy function provided the best fit to all of the Hybrid data. The mean prediction error estimates computed by the Bertalanffy function were not significantly different from the estimates of the Richards, Brody and Logistic functions in the unadjusted data but were significantly different from the estimates of the Richards and Brody functions in the adjusted Hybrid data. All mean prediction errors were small and had low standard errors. In general, the weight at 44 months was predicted well by all growth functions with the Bertalanffy function having the smallest mean prediction errors.

56 months: At 56 months (ie. adult) the Richards function provided the best prediction of weight in the

unadjusted data followed by the Brody, Bertalanffy and Logistic. The mean prediction error estimated by the Richards function was significantly lower than those from the Bertalanffy and Logistic functions. In the adjusted Hybrid weight data set, the Brody function ranked first followed by the Richards, Bertalanffy and Logistic functions. However the difference between the Brody and Richards were not significant. The Bertalanffy and Logistic functions provided a poorer fit in both populations because adult weight was underestimated (Table 19).

6.5.2 Comparison of fit between unadjusted and adjusted weight data within function and age

The differences between the unadjusted and adjusted mean prediction error estimates by age and function for the Hybrids are shown in Table 22.

The birth weights predicted by the Richards function for the unadjusted and adjusted data were similar in that both mean prediction error estimates were of the same magnitude but different only in sign. Adjusting the data significantly improved the fit of the Brody function and in fact provided a lower mean prediction error estimate than the Richards. The mean prediction error estimates computed by the Bertalanffy and Logistic growth functions were also

improved by adjusting the data.

The prediction of weaning weight based on the Richards and Brody functions were significantly improved by adjusting the data. No significant reduction in the mean prediction error estimates were observed by adjusting weaning weights, based on the Bertalanffy and Logistic functions.

The prediction of yearling weight was not improved by adjusting the data. The mean prediction error estimates for the unadjusted data based on the four growth functions were significantly lower than the mean prediction errors based on the same growth functions with the adjusted data.

At 20 months of age no significant differences were observed between the mean prediction error estimates based on the Richards function between the unadjusted and adjusted weights. The mean prediction error based on the Richards applied to the adjusted data was very similar to the mean prediction error computed on the same function in the unadjusted data. The mean prediction error estimated on the Brody function was significantly lower in the unadjusted data. The Bertalanffy and Logistic functions however provided a better fit to the adjusted data at 20 months of age and the differences were significant.

At 32 months of age, no significant differences between mean prediction errors of the unadjusted and adjusted data

were observed. All error estimates were large during this age. The mean prediction errors estimated for the adjusted data based on the Logistic function were lower when compared to the mean prediction error estimate in the unadjusted weight data, but the differences were not significant.

Mean prediction error estimates based on the four functions and applied to the unadjusted and adjusted weight data were similar at 44 months of age.

At 56 months of age mean prediction errors based on the Richards function were significantly higher for the adjusted data. However no significance was observed between mean prediction error estimates based on the Brody, Bertalanffy and Logistic functions between unadjusted and adjusted data.

6.5.3 Comparison of the variation between unadjusted and adjusted data

The standard deviations of the mean prediction error estimates within function and breed group for the unadjusted and adjusted data are given in Table 23.

Adjusting the data for year and age of dam reduced the variation in the mean prediction error estimate for birth weight in all growth functions thereby improving the fit.

At weaning, variation in the mean prediction error was

Table 23. Standard deviations of mean prediction error by function and age for the unadjusted and adjusted data from the Hybrid breed group

		Standard deviations (%)			
Age	Data	Richards	Brody	Bertalanffy	Logistic
Birth	Unadj.	13.208	15.723	18.619	30.134
	Adj.	12.576	12.482	15.656	25.548
Weaning	Unadj.	13.782	12.655	11.594	11.400
	Adj.	12.948	12.985	11.868	11.051
Yearling	Unadj.	12.428	12.272	12.271	12.034
	Adj.	12.853	12.868	12.497	11.976
20 mon.	Unadj.	8.531	8.735	9.052	9.308
	Adj.	10.958	10.947	11.285	11.747
32 mon.	Unadj.	13.390	13.626	13.793	13.971
	Adj.	11.670	11.695	11.776	11.855
44 mon.	Unadj.	10.626	10.603	10.421	10.323
	Adj.	10.010	10.013	9.794	9.630
56 mon.	Unadj.	9.558	9.360	9.020	8.853
	Adj.	9.031	9.040	8.699	8.490

reduced by adjusting the data in all but the Bertalanffy function but the improved fit was only observed with the Richards. No reduction in the variance by adjusting was observed at yearling age.

The standard deviation of the mean prediction error estimates of all functions at 20 months of age were lower for the unadjusted data compared with the adjusted data. Hence, the predicted 20 month weights were closer to the observed in the unadjusted data.

A reduction in the standard deviation by adjusting the data was observed at 32 months for all functions. However, weight was poorly described at this age although the variation in the mean prediction error estimates were reduced by adjusting the data.

The standard deviations of the mean prediction error remained almost constant at 44 and 56 months of age in the unadjusted and adjusted weight data based on the 4 functions.

6.5.4 Estimation of the consistency of fit

Table 24 shows the mean prediction errors at each age derived from the Richards, Brody, Bertalanffy and Logistic growth functions for the unadjusted and adjusted data from

Table 24. Duncan's test showing significance between mean prediction error estimates at 7 ages based on four growth functions - Hybrid

Function	Data	Birth	Weaning	Yearling	20 mon.	32 mon.	44 mon.	56 mon.
Richards	Unadj.	0.673bc	-5.115a	-0.240bc	2.002c	-6.950a	-1.355b	0.936bc
	Adj.	-0.633bc	-0.327c	-2.861b	2.055d	-8.394a	-1.488bc	3.025d
Brody	Unadj.	-18.238a	2.460d	-0.209c	-0.456c	-8.843b	-1.088c	3.108d
	Adj.	0.118c	-0.645c	-2.855b	2.135d	-8.352a	-1.526bc	2.932d
Bertalanffy	Unadj.	-40.000a	10.500f	-0.943d	-4.086c	-10.635b	0.731d	6.712e
	Adj.	-25.285a	9.206f	-3.304c	-0.603d	-8.774b	0.783d	6.667e
Logistic	Unadj.	-126.589a	12.762f	1.179d	-7.262c	-11.571b	1.706d	8.488e
	Adj.	-104.438a	14.754b	-1.732d	-3.433c	-9.151b	2.499e	8.933f

Mean prediction errors with different alphabetic letters in rows are significant $P<0.05$

the Hybrid breed group.

In the unadjusted data the Richards function showed the least significant differences between mean prediction error estimates ranging from -6.9 to 2.0 and falling into three significance classes with much overlap. The mean prediction errors estimated from the Brody function were spread over a wider range and showed greater significant differences between ages; means were grouped into four significance classes. The mean prediction error estimates of the Bertalanffy and Logistic functions fell into six significance classes, suggesting that the functions provided a less consistent fit from birth to 56 months.

In the adjusted data the mean prediction errors based on the Richards function ranged from -8.4 at 32 months of age to 3.0 at 56 months of age falling into four significance classes. The mean prediction error estimates computed by the Brody function in the adjusted data fell into four significance classes, and therefore the Brody was as consistent as the Richards function. The Bertalanffy function was very inconsistent in predicting small and similar mean prediction error estimates; the mean prediction error estimates fell into six significance classes. The Logistic function followed the same trend as the Bertalanffy and in addition, the mean prediction error estimates applied to the adjusted data were in six significance classes.

6.5.5 Conclusions

The Richards was the only function that provided a good and uniform fit to all of the birth weight data among Hybrids; the function predicted birth weight with less than ± 0.7% mean prediction error in all of the data sets. The Brody provided a differential fit at birth providing mean prediction errors that were small and similar to the Richards in the adjusted data but significantly different from the Richards in the unadjusted Hybrid data. The Bertalanffy and Logistic functions were very poor in describing birth weight in both of the Hybrid data sets.

Weaning weight was best described by the Brody function. Significant differences in the mean prediction error estimates were observed between the means computed on the Richards and Brody function in the unadjusted data while the mean prediction errors were small and similar in the adjusted data. Thus, the Richards and Brody functions described weaning weight adequately.

Yearling weight was uniformly described by all four growth functions with mean prediction errors that were similar in each set of data.

The Bertalanffy function provided the lowest estimate

of error at 20 months of age in the adjusted data while the Brody function provided a good description of weight at 20 months in the unadjusted data. The Richards, Brody and Bertalanffy functions all provided an adequate fit at 20 months of age.

Weight at 32 months was overestimated by all growth functions as they were insensitive to temporary and sudden changes in weight. High standard errors were also associated with the mean prediction error estimates during this period.

All growth functions described 44 month weight adequately. In general, during the intermediate ages (yearling to 44 months) all functions fitted the data well.

Adult weight was best described by the Brody and Richards functions poorly described by the Bertalanffy and Logistic functions.

Adjusting the data for year and age of dam significantly improved the fit of the Brody, Bertalanffy and Logistic functions at birth by reducing the mean prediction errors and the variance. The prediction of weight and fit of the Richards and Brody functions were significantly improved at weaning, by adjusting the Hybrid weight data. However, the fit of the functions at the yearling stage was significantly better with the unadjusted data. Adjusting

the weights after 20 months of age did not significantly reduce the mean prediction error estimates with the exception of the Logistic function at 32 months.

Thus, the value of adjusting the Hybrid data was limited to improving the fit of the functions during the pre-yearling ages. A better fit was often associated with a reduction in the variance of the mean prediction error estimates.

The Richards function provided a very uniform estimation of mean prediction errors in each Hybrid data set. The prediction error estimates ranged within narrow limits, were small in magnitude and fell into a lower number of significance classes compared with the other three growth functions. The mean prediction errors based on the Brody function ranked second with respect to the consistency of fit between ages, and the uniformity was pronounced in the adjusted data. The Logistic and Bertalanffy functions were very inconsistent with variable mean prediction errors at each age.

6.6 Analysis of Hereford data

6.6.1 Analysis of the goodness of fit of each growth function applied to each age

Table 25 shows the mean prediction error estimates, standard errors and differences between unadjusted and adjusted mean prediction error estimates by function at each age for the Hereford breed group.

The minima and maxima for the % mean prediction error by function and age for the Hereford data sets are shown in Appendix Table 2.

Birth: The Richards function provided the best prediction of birth weight in the unadjusted Hereford data much like the observations in the Hybrid breed group (see Table 22) and underestimated birth weight slightly while the other functions overestimated it. The Bertalanffy and the Logistic functions were particularly poor in predicting birth weight. The mean prediction error estimates calculated on all functions were significantly different from each other. In the adjusted Hereford weight data a similar trend was recognised with the Richards function providing a good prediction of birth weight followed by the Brody, Bertalanffy and Logistic functions.

Weaning: The lowest mean prediction error for Herefords

Table 25. Mean prediction error estimates and standard errors (Se) for unadjusted and adjusted Hereford data and differences

Age	Number of Animals	Function	Mean Prediction Error (%) [1]	Se. (%) [1]	Mean Prediction Error (%) [2]	Se. (%) [2]	Difference
Birth	144 [1]	Richards	1.659a	1.099	0.340a	0.744	1.319
		Brody	-5.489b	1.179	10.662b	0.667	-16.151**
	319 [2]	Bertalanffy	-28.435c	1.435	-15.118c	0.859	-13.317**
		Logistic	-108.392d	2.328	-85.529d	1.385	-22.863**
Weaning	144	Richards	-5.940ab	1.413	-2.064a	0.876	-3.876**
		Brody	-2.869a	1.366	-7.016b	0.911	4.147**
	307	Bertalanffy	-6.806b	1.227	4.357c	0.829	-11.163**
		Logistic	8.945c	1.222	10.859d	0.761	-1.914
Yearling	137	Richards	-0.137a	0.769	-1.621a	0.433	1.484
		Brody	-0.073a	0.764	-1.561a	0.443	1.488
	339	Bertalanffy	-0.034a	0.756	-1.765a	0.422	1.731
		Logistic	1.970b	0.741	-0.545a	0.400	2.515*
20 months	126	Richards	-0.286a	0.838	0.644ab	0.525	-0.930
		Brody	-0.635a	0.845	1.808a	0.517	-2.443*
	206	Bertalanffy	-4.064b	0.874	-1.008b	0.535	-3.056**
		Logistic	-7.596c	0.903	-4.240c	0.558	-3.356**
32 months	107	Richards	-5.221a	1.149	-7.280a	0.796	2.059
		Brody	-5.885ab	1.156	-6.784a	0.792	0.899
	192	Bertalanffy	-7.344ab	1.170	-7.376a	0.797	0.032
		Logistic	-8.804b	1.184	-7.273a	0.796	-1.531
44 months	89	Richards	-0.617a	1.027	-0.951a	0.785	0.334
		Brody	-0.448a	1.025	-1.647a	0.791	1.199
	147	Bertalanffy	1.286ab	1.007	0.633a	0.772	0.653
		Logistic	2.625b	0.993	3.127b	0.752	-0.502
56 months	67	Richards	1.006a	1.086	4.315ab	0.790	-3.309*
		Brody	1.913a	1.075	2.832a	0.802	-0.919
	102	Bertalanffy	5.732b	1.031	6.713b	0.770	-0.981
		Logistic	8.094b	1.005	9.825c	0.744	-1.731

[1] Unadjusted
[2] Adjusted
a,b,c,d - Mean prediction error estimates with different alphabetic letters within an age are significant $P<0.05$

*$P<0.05$
**$P<0.01$

at weaning was obtained for the weights based on the Brody function followed by the Richards, Bertalanffy and Logistic in the unadjusted data. The mean prediction error estimates based on the Brody and Richards functions were similar whereas, the Logistic computed an error that was significantly higher than the estimates of the Brody and Richards functions. In the adjusted Hereford weight data the mean prediction error for the Richards function was significantly lower compared to the other growth functions, and was therefore different from the trend in the Hybrid breed group (Table 22).

Yearling: At one year of age all functions described growth adequately with a minimum of error in the unadjusted data much like the results in the Hybrid breed group. Furthermore, as in the Hybrids, the Richards, Brody and Bertalanffy functions estimated yearling weight with <1% error and were significantly lower than the errors computed by the Logistic function. In the adjusted Hereford data all growth functions overestimated yearling weight with <2% error with the Logistic function providing the lowest mean prediction error.

20 months: At 20 months all functions overestimated weight with the Richards providing the lowest mean prediction error and the Logistic the highest in the unadjusted data. Significant differences were observed

between the mean prediction errors estimated by the Richards, Bertalanffy and Logistic functions while no significance was observed between the mean prediction errors of the Richards and Brody functions. Similarly, in the adjusted Hereford data the the Richards function provided the smallest mean prediction error but the estimate was not significantly different from the means based on the Brody and Bertalanffy functions. Thus, the weight at 20 months was best described by the Richards function followed by the Brody and Bertalanffy functions.

<u>32 months</u>: Large mean prediction errors and standard deviations were observed at 32 months of age in the unadjusted and adjusted Hereford data for all functions much like the trends observed among the Hybrids, for the same reasons as previously discussed.

<u>44 months</u>: The weight at 44 months of age was best described by the Brody and Richards functions followed by the Bertalanffy and Logistic functions in the unadjusted data. No significance was established between the mean prediction error estimates based on the Richards, Brody and Bertalanffy functions although the mean prediction error estimate based on the Logistic function was significantly different from the Richards and Brody functions. In the adjusted Hereford data, the fit of the functions was similar to the Hybrids (Table 22).

56 months: For the most advanced age group (56 months) the mean prediction error estimates based on the Richards and Brody functions were similar and ranged from 1-2% in the unadjusted weight data while the Bertalanffy and Logistic functions predicted 56 month weight with a significantly higher mean prediction error. Adult weight was underestimated by all functions. In the adjusted data no significance was established between the errors computed by the Richards and Brody functions and Richards and Bertalanffy functions although these values were significantly different from the mean prediction error estimates based on the Logistic function. In general, the Richards and Brody function provided a satisfactory description of 56 month weight in the unadjusted and adjusted data.

6.6.2 Comparison of fit between unadjusted and adjusted weight data within function and age

The differences between the unadjusted and adjusted mean prediction error estimates by age and function for the Herefords are shown in Table 25.

The mean prediction error estimates at birth calculated on the Brody, Bertalanffy and Logistic functions differed significantly between the unadjusted and adjusted Hereford

weight data while no significance was established on the mean prediction errors based on the Richards function. Adjusting the data did not improve the fit of the Brody function at birth although the fit of the Bertalanffy and Logistic functions was improved.

At weaning the mean prediction errors based on the Richards function were reduced significantly by adjusting the data while the reverse occurred with respect to the Brody function.

The differences between mean prediction error estimates calculated on the Richards, Brody and Bertalanffy functions for the unadjusted and adjusted data, at yearling were not significant. The mean prediction error estimates based on the Logistic function were significantly lower in the adjusted data compared with the unadjusted data. The growth functions in general provided a better fit to the unadjusted yearling weights.

At 20 months of age the mean prediction error estimates based on the Richards function between the unadjusted and adjusted data were not significantly different although the Brody function provided a better fit to the unadjusted data. The fit of the Bertalanffy and Logistic functions was significantly improved by adjusting the data.

For all other ages, the mean prediction error estimates

of the unadjusted and adjusted data within function were similar with the exception of the mean prediction errors based on the Richards function at 56 months of age where a better fit to the unadjusted Hereford data was observed.

6.6.3 Comparison of the variation between unadjusted and adjusted data

Table 26 shows the standard deviations of mean prediction errors for the unadjusted and adjusted data by function and age for the Hereford breed group. The Brody, Bertalanffy and Logistic functions fitted to the adjusted data reduced the variation in the mean prediction error estimates at birth and a reduced variation was associated with a closer fit of the models. The variation in the unadjusted and adjusted data remained unchanged for the Richards function.

At weaning, although the variation in the mean prediction error estimates was reduced by adjusting the data based on the Richards, Brody and Logistic functions, the mean prediction error was only improved in the Richards (Table 25).

At yearling age adjustment of the data reduced the variation of the mean prediction errors in all functions significantly improved the fit of the Logistic function

Table 26. Standard deviations of mean prediction error by function and age for the unadjusted and adjusted data from the Hereford breed group

Age	Data	Standard deviations (%)			
		Richards	Brody	Bertalanffy	Logistic
Birth	Unadj.	13.184	14.143	17.218	27.940
	Adj.	13.285	11.909	15.346	24.732
Weaning	Unadj.	16.952	16.387	14.719	14.662
	Adj.	15.351	15.968	14.529	13.331
Yearling	Unadj.	12.724	12.653	12.509	12.265
	Adj.	11.284	11.533	10.922	10.429
20 Months	Unadj.	9.402	9.487	9.807	10.130
	Adj.	10.667	10.505	10.866	11.337
32 Months	Unadj.	11.888	11.959	12.105	12.252
	Adj.	11.027	11.976	11.037	11.029
44 Months	Unadj.	9.688	9.671	9.501	9.371
	Adj.	9.522	9.595	9.364	9.119
56 Months	Unadj.	8.890	8.801	8.441	8.223
	Adj.	7.974	8.101	7.772	7.511

(Table 25).

At 20 months of age adjusting the data increased the variation of error in the data while at 32 and 44 months of age the variation in the estimate was similar between the unadjusted and adjusted data. The variation in the Hereford data based on all functions was somewhat reduced by adjusting the weights at 56 months but the reduced variation was not associated with a reduction in the mean prediction errors (Table 25).

6.6.4 Estimation of the consistency of fit

Table 27 shows the mean prediction errors at each age based on the Richards, Brody, Bertalanffy and Logistic growth functions for the unadjusted and the adjusted data from the Hereford population.

The mean prediction error estimates based on the Richards function ranged from -5.9 to 1.7 in the unadjusted data, falling into two significance classes while the mean prediction errors based on the Brody function showed a slightly wider range from -5.9 to 1.9 and fell into three significance classes. The mean prediction error estimates based on the Bertalanffy function fell into four significance classes while the Logistic function was least consistent and the mean prediction errors classified into

Table 27. Duncan's test showing significance between mean prediction error estimates at 7 ages based on four growth functions - Hereford

Function	Data	Birth	Weaning	Yearling	20 Mon.	32 Mon.	44 Mon.	56 Mon.
Richards	Unadj.	1.659b	-5.940a	-0.137b	-0.286b	-5.221a	-0.617b	1.006b
	Adj.	0.340c	-2.064b	-1.601c	0.644c	-7.280a	-0.951bc	4.315d
Brody	Unadj.	-5.489a	-2.869ab	-0.073c	-0.635bc	-5.885a	-0.448bc	1.913c
	Adj.	10.662d	-7.016a	-1.561b	1.808c	-6.784a	-1.647b	2.832c
Bertalanffy	Unadj.	-28.435a	6.807d	-0.034c	-4.064b	-7.344b	1.286c	5.732d
	Adj.	-15.178a	4.357e	-1.765c	-1.078cd	-7.376b	0.633d	6.713e
Logistic	Unadj.	-108.392a	8.946d	1.976c	-7.596b	-8.084b	2.625c	8.094d
	Adj.	-85.529a	10.859f	-0.545d	-4.240c	-7.273b	3.127e	9.825f

Mean prediction errors with different alphabetic letters in rows are significant $P<0.05$

four significance classes, with a wider range in the error estimates.

In the adjusted data the Richards means ranged from -7.3 to 4.3 falling into four significance classes. The mean prediction error estimates based on the Brody showed a still wider range falling into four significance classes. Thus, the Richards provided a more consistent fit than the Brody across ages. The mean prediction error estimates based on the Bertalanffy showed a much wider range than the Richards and Brody falling into five significance classes while means based on the Logistic fell into six significance classes.

6.6.5 Conclusions

The Richards was the only model that provided a consistently good prediction of birth weight in both sets of the Hereford weight data. The Bertalanffy and Logistic functions were very unreliable in predicting birth weight accurately.

The Brody function provided a low mean prediction error estimate in the unadjusted Hereford data and the Richards provided a significantly lower mean prediction error in the adjusted data at weaning.

Yearling weight was predicted well by all four growth functions in the data sets with the Brody function estimating it with a consistently low mean prediction error.

The weight at 20 months of age was estimated accurately by the Richards and Brody functions in the unadjusted data and in addition by the Bertalanffy function in the adjusted data.

Weight at 32 months was overestimated by all functions and none of the growth models could adjust to the temporary weight loss.

At 44 months of age, the Richards, Brody and Bertalanffy functions predicted weights with a minimum of error and the Bertalanffy provided the lowest mean prediction error to the adjusted data.

At 56 months the Richards and Brody models provided a good fit to the unadjusted Hereford data and the mean prediction error estimates based on the same functions were higher but not significantly different between functions in the adjusted data.

Adjusting the data did not significantly improve the fit of the Richards function at birth although the mean prediction error estimates were reduced. However the fit of the Brody function was significantly decreased by adjusting

the data and is contrary to what was observed among the Hybrids. The fit of the Bertalanffy and Logistic functions at birth was improved by adjusting the data. The fit of the Richards function was improved by adjusting the data at weaning. Adjusting the data had no effect in improving the fit of the four growth functions at any of the subsequent ages, with the exception of the Bertalanffy and Logistic functions at 20 months of age.

The consistency of fit based on a Duncan's comparison of means showed that the Richards function was most consistent in estimating mean prediction errors which were small and uniform within each set of Hereford data across ages.

6.7 Analysis of data from the XB groups

6.7.1 Analysis of the goodness of fit of each growth function applied to each age

The mean prediction error estimates, standard deviations, standard errors, minima and maxima for the seven ages by function for the 100% BR, 75% BR, 50% BR 50% LD and 75% LB breed groups are shown in Appendix Tables 3 to 6. The results show exceptional similarity to the two large breed groups with the Richards consistently providing a good prediction of birth weight, the Brody providing a less

consistent fit at birth and the Bertalanffy and Logistic functions providing a poor fit at birth. The weaning weights were predicted satisfactorily by the Richards and Brody functions while yearling weight was predicted well by all functions in each breed group. Weight at 56 months was predicted well by the Richards and Brody functions.

6.7.2 Estimation of the consistency of fit

Mean prediction error estimates arranged in a Duncan's table derived from the Richards, Brody, Bertalanffy and Logistic functions for the 100% BR, 75% BR, 50% BR 50% LD and 75% LB breed groups are shown in Appendix Tables 7 to 10. The Richards function provided a uniform estimation of error in the 100% BR, 50% BR 50% LD and 75% LB breed groups followed by the Brody which provided an equally consistent fit. In the 75% BR breed group the Brody function followed by the Richards provided the most consistent fit across ages.

6.7.3 Conclusions

The Richards function provided a good estimate of birth weight, weaning weight and adult weight while the Brody function showed an inconsistent fit at birth and a good fit at weaning and 56 months of age. The fit of the four models

during the intermediate ages was similar and followed the same patterns as in the larger breed groups. In general, the Richards and Brody functions were consistent in predicting with small and similar mean prediction error estimates across ages which was similar to the observations in the two larger breed groups.

6.8 Correlations between parameter estimates for the Richards and Brody functions

The simple correlations between parameters (A), (B), (k), (M), (AGR6), (AGR12), (AGR18) and (Y*) from the Richards model fitted to the Hybrid and Hereford lines are shown in Table 28 and for the Brody model in Table 29. Correlations were computed using adjusted data.

Correlations between (A) and (k) based on the Richards and Brody growth functions were similar in both Hybrid and Hereford breed groups ranging from -0.53 to -0.66 indicating early maturing animals grew to smaller adult weights. Similar relationships were reported by Brown et al. (1976) in Jersey and Hereford females, and by Fitzhugh and Taylor (1971) with Herefords. Thus, selection for early maturing types should lead to correlated responses in reducing adult body weight. In the present analysis the maximum difference in correlations between parameters (A) and (k) in the two breed groups based on the Richards and Brody functions was

Table 28. Correlations between growth parameters from the Richards model fitted to the Hybrid adjusted data (above diagonal) and Hereford adjusted data (below diagonal)

	(A)	(B)	(k)	(M)	(AGR6)	(AGR12)	(AGR18)	(Y*)
(A)	-	0.41*	-0.65**	-0.45**	-0.12	0.04	0.47**	0.36
(B)	0.47**	-	-0.86**	-0.98**	-0.73**	-0.71**	-0.31*	-0.97**
(k)	-0.66**	-0.88**	-	0.91**	0.80**	0.66**	0.16*	0.52*
(M)	-0.45**	-0.99**	0.87**	-	0.80**	0.78**	0.31*	0.97**
(AGR6)	-0.17	-0.56**	0.76**	0.57**	-	0.94**	0.64**	0.63*
(AGR12)	-0.21	-0.76**	0.80**	0.76**	0.84**	-	0.84**	0.74*
(AGR18)	0.17	-0.39*	0.30*	0.39*	0.43**	0.78**	-	0.48*
(Y*)	-0.21	-0.73**	0.70**	0.80**	0.43*	0.53*	-0.17	-

*P<0.05
**P<0.01

Table 29. Correlations between growth parameters from the Brody model fitted to the adjusted Hybrid data (above diagonal) and adjusted Hereford data (below diagonal)

	(A)	(B)	(k)	(AGR6)	(AGR12)	(AGR18)
(A)	-	0.36	-0.53**	0.48**	0.93**	0.95**
(B)	-0.13	-	0.19	0.40*	0.28*	0.09
(k)	-0.58**	0.07	-	0.45**	-0.29*	-0.73**
(AGR6)	0.34*	0.16	0.53**	-	0.72**	0.27*
(AGR12)	0.88**	0.12	-0.23*	0.70**	-	0.87**
(AGR18)	0.96**	0.04	-0.73**	0.19	0.83**	-

*P<0.05
**P<0.01

0.05. In a preliminary analysis, using the unadjusted weight data, the difference in the correlations between the parameters (A) and (k) based on the Richards function between lines was 0.14 (see Appendix Table 11). Furthermore, the % difference between the maturing rates (k) of the Hybrid and Hereford lines based on the Richards function was 17.1% for the adjusted weights (Table 18) while there was an 8.82% difference in their asymptotes. Brown et al (1976) observed a) wider differences between correlations of (A) and (k) between breeds and b) a greater percentage difference in the maturing rates compared to the asymptotes between two breeds and they were of the opinion that the parameters (A) and (k) are relatively independent. However from the results of the present analysis there is little evidence to suggest that the two parameters are independent.

In the Hybrid breed group correlations between (A) and (AGR) based on the Richards function changed from negative to positive (r=0.47) as the age increased from 6 to 18 months. A similar trend was observed in the Hereford breed group although, the correlation of (A) and (AGR18) was slightly less positive compared to the Hybrids. Thus, animals with lower than average growth rates during the post weaning to yearling ages (6 to 12 months) grew faster relative to its mature weight, and animals with higher growth rates at 18 months were again heavier at maturity.

Correlations between (A) and (AGR) based on the Brody function fitted to the two breeds were significant and positive at 6, 12 and 18 months of age, with the values increasing with age. Animals with higher growth rates at later ages were therefore more likely to achieve higher mature weights than animals with higher growth rates at early ages.

Correlations between (A) and (AGR6) based on the Richards function were negative ($r = -0.12$ and -0.17) for the adjusted Hybrid and Hereford data, respectively, although the values were not significant. However, in both breed groups (AGR6) was positively correlated with the maturing rate parameter (k) ($r=0.80$ and $r=0.76$) suggesting that early maturing animals with higher gains at 6 months of age grow to smaller mature weights. The same effect was less pronounced in the Hybrid line when gain at 12 months of age was considered, as the correlations between (A) and (AGR12) were less negative and the correlations between (k) and (AGR12) less positive. The relationships were reversed at 18 months of age as the correlations between (A) and (AGR18) were positive ($r=0.47$ and $r=0.17$) in Hybrid and Hereford lines, while the correlations between (AGR18) and (k) were less positive ($r=0.16$ and $r=0.30$) in the same two lines. The correlations between (A), (AGR18) and (k) suggested that late maturing types with higher growth rates

at 18 months of age had higher mature or adult weights. Brown et al (1976) found early maturing types with higher growth rates at the point of inflection grew to smaller mature weights.

Based on the Brody function, animals with a slower general maturing rate and rapid growth rates after 1 year of age were heavier at maturity.

According to the formulae of the models when (M) increases (Y*) should increase and this is shown by the high and positive correlations between the two parameters. It would therefore suggest that populations which are characterised by higher absolute values for (M) are heavier at inflection.

The correlations between (A) and (M) were negative with values of -0.45 in both breed groups. Thus, the correlations between (Y*) and (A) was variable between breeds, ranging from -0.21 in the Hereford breed to 0.36 in the Hybrid breed. A positive correlation between (Y*) and (A) in the Hybrid line suggested that heavier animals at inflection were heavier at maturity. However, the correlation between (Y*) and (A) was not significantly different from zero. The correlations between (Y*) and (A) may again be influenced by the absolute values of (A), as (Y*) is a function of (A) and (M). Fitzhugh (1976) stated

that it is often difficult to interpret relationships based on algebraic models as characters are not completely independent, and often relationships contrary to a basic biological trend are obtained.

The correlations between (k) and (AGR6) were high, ranging from 0.76-0.89 in both breed groups based on the Richards and Brody functions, suggesting that early maturing types grow rapidly to 6 months of age. The correlations between (k) and (AGR12) based on the Richards function were less positive in both breed groups. The correlations between (k) and (AGR12) based on the Brody function and applied to the two breed groups was negative. Based on the Richards function, in the Hybrid and Hereford lines the correlations between (k) and (AGR18) were slightly positive with values of 0.17 and 0.30 respectively. At 18 months the correlations between (k) and (AGR) based on the Brody function applied to the breeds were negative indicating that at 18 months early maturing types had lower absolute daily gains. In general, early maturing animals were characterised by faster growth rates during early ages and slower growth rates at later ages.

Weight at the point of inflection (Y*) was positively correlated with (AGR6) in all of the data and negatively correlated with (AGR18) in the Hereford line suggesting that Herefords heavier at inflection had higher growth rates at 6

months of age but lower growth rates at 18 months of age. The same result was not observed among the Hybrids.

The correlations between (M) and (k) were high and positive along with the correlations between (M) and (Y*). This would suggest that early maturity was thus associated with higher values for (M) and higher inflection weights.

The correlations between (M) and (AGR) at 6, 12 and 18 months showed the same trend as for the correlations between (k) and (AGR) within each breed group. Thus, heavier animals at inflection showed higher growth rates at 6 months of age but relatively lower growth rates at 18 months of age.

Interrelationships between growth rates at different ages have often been investigated on actual data and Fitzhugh and Taylor (1971) observed that a higher growth rate during one period was accompanied by a lower growth rate in another. Based on the Richards model, in both the Hybrid and Hereford data the correlations between (AGR6) and (AGR12) were high, ranging from 0.94 to 0.79. The correlations between (AGR6) and (AGR12) based on the Brody model were lower ranging from 0.72 to 0.39. Similarly the correlations between (AGR12) and (AGR18) were always positive; the correlations based on the Brody model being somewhat higher. Thus, selection for growth rate at 6

months should increase growth rate at 12 months, and selection for an increased growth rate at 12 months should increase growth rate at 18 months of age. However, as the age interval increases the degree of association decreased. Thus, when ages are widely separated, selection for a high growth rate at the lower age would not be expected to rapidly improve growth rate at the higher age.

6.8.1 Conclusions

In all derived biological models the relationship between the maturing rate and mature weight was negative suggesting that lighter animals at maturity are early maturing. Early maturing types had absolute growth rates that were above average at early ages (6 months) and below average at later ages (18 months), suggesting that selection for growth rate at early ages would increase maturing rate.

Based on correlations of the Richards model animals with higher adult body weights grew more slowly at 6 and 12 months of age and grew faster than average at 18 months although growth rates were relative to adult body weight. Based on the Brody model, animals with higher growth rates after 12 months were expected to be heavier at maturity. Furthermore, early maturing animals with higher gains at 6 months grew to smaller mature weights and late maturing

animals with higher gains at 18 months grew to larger mature weights.

Absolute growth rates were positively correlated when the two ages were closely adjacent but less positively correlated when widely separated suggesting that selection for increased growth rates would not necessarily improve growth rate to the same extent at subsequent ages especially if the two ages are widely separated.

6.9 Analysis of absolute growth rates

Table 30 contains the observed absolute growth rates (AGR), the predicted absolute growth rates based on each growth function, and the differences between the observed and predicted growth rates by growth period and breed group for the adjusted data from the Hybrid and Hereford lines.

Figures 9 and 10 show the observed and predicted absolute growth rates by function and breed group for the adjusted data.

The highest observed absolute growth rates (average daily gain) were recorded during the pre-weaning stage in both breed groups; post-weaning to yearling gains were somewhat lower than the pre-weaning gains and the drop was greater among the Hybrid heifers. The growth rates increased again during the yearling to 18 month period in

Table 30. Mean observed and predicted absolute growth rates kg/day and difference $(Y-\hat{Y})$ by function and breed group over 4 growth periods

	Absolute growth rate kg/day (AGR)							
	Birth-Wean		Wean-Yrl.		Yrl.-18 Mon.		18 Mon.-Adult	
Function	HY	HE	HY	HE	HY	HE	HY	HE
Observed (Y)	0.890	0.739	0.486	0.536	0.657	0.600	0.086	0.086
Richards (YR)	0.850	0.723	0.586	0.580	0.388	0.392	0.105	0.096
Brody (YB)	0.855	0.788	0.584	0.545	0.386	0.366	0.106	0.105
Bertalanffy (YV)	0.698	0.636	0.667	0.624	0.449	0.429	0.083	0.083
Logistic (YL)	0.482	0.443	0.662	0.627	0.544	0.523	0.066	0.063
Difference $(Y-\hat{Y})$								
Y-YR	0.040	0.016	-0.100	-0.044	0.269	0.208	-0.019	-0.010
Y-YB	0.035	-0.049	-0.098	-0.009NS	0.271	0.234	-0.020	-0.019
Y-YV	0.192	0.103	-0.181	-0.088	0.208	0.171	0.003NS	0.003NS
Y-YL	0.408	0.296	-0.176	-0.091	0.113	0.077	0.020	0.023

All standard errors of means were <0.007

All differences $(Y-\hat{Y})$ were significant at P<0.01 except the values denoted by a NS

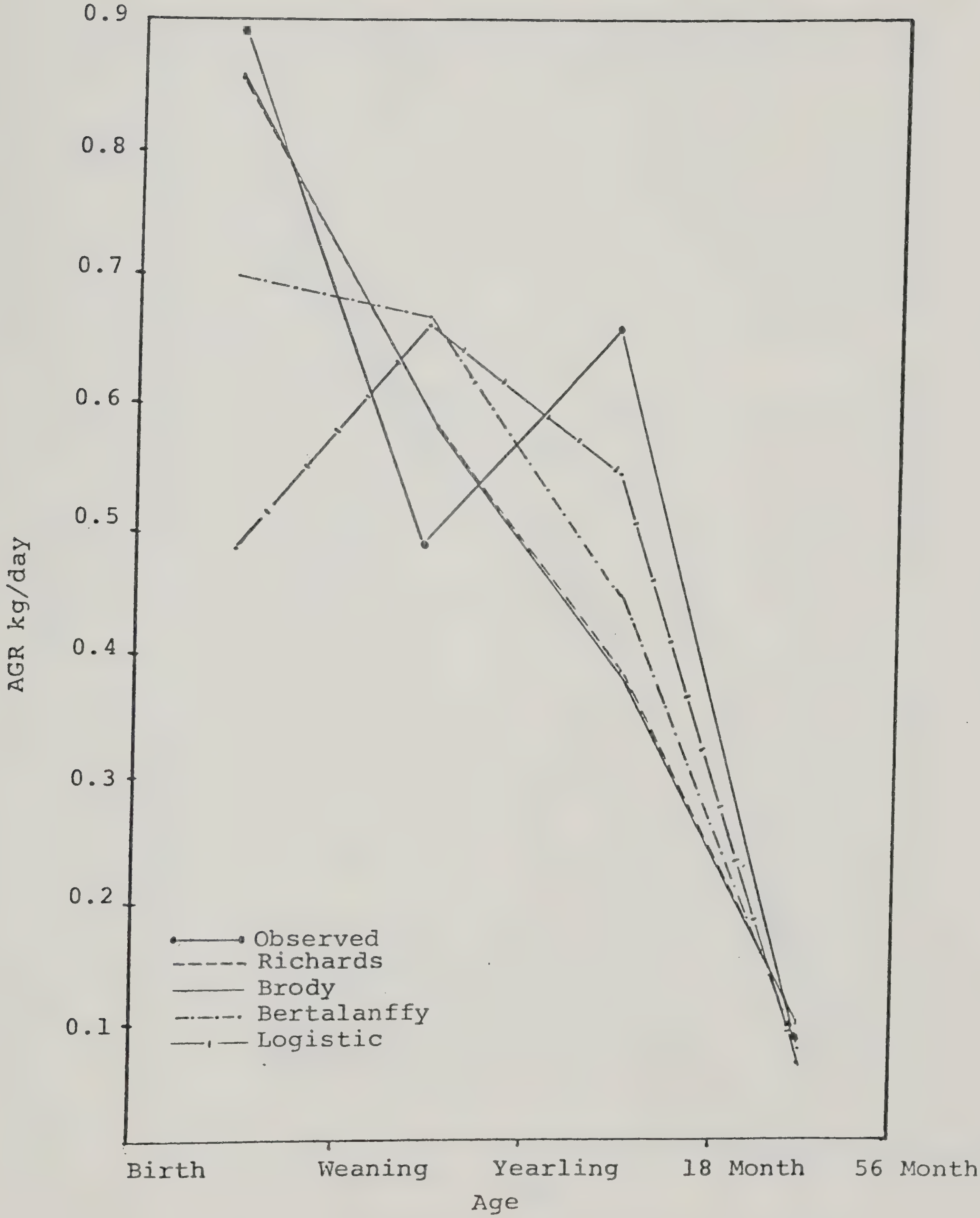

Fig. 9. Observed and predicted AGR - Hybrid

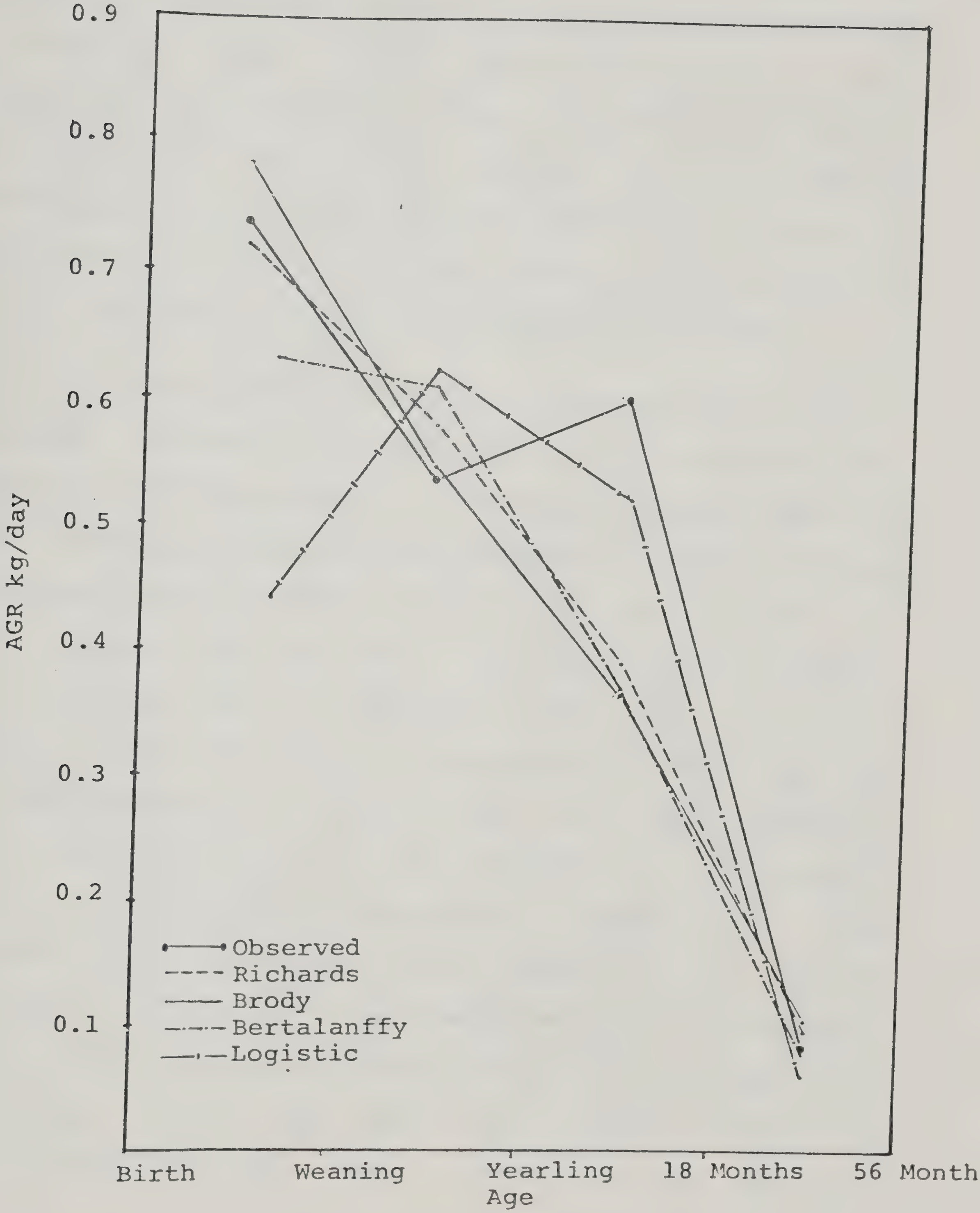

Fig. 10. Observed and predicted AGR - Hereford

both groups and dropped to a minimum during the stage from 18 months to adult. The cascading effect seen to occur in growth rate between adjacent periods was also observed by Fitzhugh and Taylor (1971). The absolute growth rates predicted by the Richards, Brody, Bertalanffy and Logistic functions were significantly different from the observed ($P<0.01$). In both breed groups the variations in season and management accounting for weight changes limited the use of growth functions in predicting absolute growth rates.

During the period from birth to weaning the Richards function predicted mean absolute growth rates with a 4.7% and 2.2% error in relation to the observed growth rates in the Hybrid and Hereford lines respectively while the Brody function predicted absolute growth rates with a 4.1% and 6.6% error in the same lines. The Bertalanffy and Logistic functions were poor in predicting gains during the pre-weaning stage due to an overestimation of birth weight and an underestimation of weaning weight. All growth functions, with the exception of the Brody applied to the Hereford line, underestimated pre-weaning absolute gain. The overestimation based on the Brody function of gain in the Hereford line was due to an underestimation of birth weight and an overestimation of weaning weight which increased the difference between the observed and predicted weights. In the Hereford line the closest approximation of the mean

observed pre-weaning gain was seen with the Richards function when birth weight was slightly underestimated and weaning weight was slightly overestimated.

During the post-weaning to yearling period all functions applied to the Hybrid data overestimated absolute growth rates; the Richards by 20.6%, Brody 20.2%, Bertalanffy 37.2% and the Logistic by 36.2%. The growth rate predicted by the Brody function for the Hereford data fitted very well. Furthermore, as there appeared a general overestimation of daily gains during this period, the growth rates computed by each of the functions were closer to the observed growth rates among the Hereford heifers as they showed higher growth rates during the feed test period which followed weaning.

The deviations of the predicted gains from the observed were high during the yearling to 18 month period in both lines; observed daily gains were also higher compared to the preceeding stage in both lines as the period coincided with summer when the heifers generally showed greater increases in body weight. Due to this temporary environmental effect that increased weight gain over the period, greater differences were observed between the predicted and observed gains, all functions underestimating growth rates in both breeds.

The predicted daily gains during the last stage were in closer agreement with the observed daily gains as growth rate was more uniform and the time interval large.

A similar analysis was done for mean gain over period comparing the observed weight gain and the expected weight gain using each growth function. Appendix Table 12 shows the mean weight gain over the period and the differences between observed and predicted weight gains by breed group and function. The results were similar to the analysis of absolute growth rates.

As growth functions regress size on age and are of an exponential decay type, they are poor in adjusting for fluctuations conditioned by management practices and environment, often seen in biological data. The gains predicted on these models assume a progressive decline in growth rate at each period and thus the two functions that provided a good fit to the data, i.e. Richards and Brody almost follow a straight line across all periods (Figures 9 and 10). A display of the observed gains by a linear regression of growth rate on age with the seasonal effects removed would have afforded a worthwhile but more theoretical appraisal reflecting the genetic trends in absolute growth rates of the population. Furthermore, by this technique the observed gains at each period could have

been more appropriately compared with the predicted growth rates based on the 4 growth models.

6.9.1 Conclusions

The Richards and Brody functions provided estimates of predicted preweaning absolute growth rates to the adjusted data from the Hybrid and Hereford lines which limited the mean error to <7%. The Brody function was particularly efficient in predicting mean absolute gains similar to the gains observed in the Hereford line during the weaning to yearling period. All growth models were poor in predicting absolute gains during the yearling to 18 month period. The absolute gains predicted by the four growth functions were quite similar to the observed gains during the last growth period even though, only the predicted absolute gains based on the Bertalanffy function were not significantly different from the observed absolute gains in both breed groups.

7. OVERVIEW

The four parameter Richards model as well as the simpler 3 parameter Brody model fitted all of the data better than the Bertalanffy and Logistic models. The Bertalanffy and Logistic models provided a poor fit as birth weight was always overestimated and adult weight underestimated. However, none of the functions could account for seasonal fluctuations that reduced body weight.

A growth curve that provides a good fit to a set of longitudinal observations of a single animal or population reflects the genotype of the animal or population and selection for growth traits on a predicted growth curve may be carried out if the curve is adjusted for temporary environmental conditions. In any animal improvement program which is founded on the principles of breeding and selection as a basis of improvement, selection for growth traits reflect changes in the shape of the basic growth curve. Selection for pre and post weaning growth rate, which is a common practice in essence selects positively for an increased maturing rate. Furthermore, growth rate and body weight within a stage of growth is positively correlated especially at early ages (Fitzhugh and Taylor, 1971). By selecting for increased growth rates prior to 1 year of age, weight at that age and maturing rate are increased while mature weight may be decreased. However the increased

growth rate is only relative to mature size. If the effects of selecting for increased growth rates were to be shown on a cumulative growth curve, the slope of the curve prior to inflection would be increased and the slope post inflection decreased. From this discussion it is very evident that the time at which beef animals are marketed becomes important, in order to take advantage of these growth characteristics, as it becomes less economical to keep animals well past their peak growth periods.

In the recent past the effect of cow size and production efficiency has been emphasized (Long et al., 1975a; Morris and Wilton, 1976). Selection for an increased maturing rate may be one method of reducing size as it is negatively correlated with mature weight. However, as the mature body size or adult weight is highly heritable unless selection is intense the rate of progress would be slow. Theoretically, selection for increased adult body size on the other hand will have opposite effects and would select late maturing types in which the change of the slope of the cumulative growth curve would be more gradual. It must be, however, born in mind that the preceeding discussion is limited to selection within a breed and should not be confused with slow or fast maturing breeds of cattle.

Indirect selection for increased maturing rates can also have an effect on carcass quality. Ideally, a beef

animal at the time of marketing should contain maximum muscle, and optimum fat and minimum bone (Berg and Butterfield, 1976). Animals at a higher degree of maturity would be more likely to put on fat compared to muscle, as muscle growth reaches a plateau at a smaller weight and age while fat growth can increase until the animal approaches its adult body size at which time it will plateau. Once the animal reaches adult body size which is under genetic control, the relative gain will be small.

A series of weight-age points of a longitudinal type is often difficult to interpret; one method of condensing all of the information into biologically interpretable parameters is by the use of growth curves. When the values of the fitted parameters are known, many of the commonly used growth traits such as average daily gains, instantaneous growth rates, lifetime growth rates, relative growth rates and maturing rates could be easily obtained. However, the accuracy of the derived estimates such as growth rates using the growth 'constants' (Brody, 1945) or fitted parameters depends on how well the function of choice fits the data at each of the selected data points. Once the function of choice has been identified the data generated by the function can be used as an alternative to the true biological model as if it was known (Brown et al., 1976).

An appropriate method of estimating the fit of a growth

model is still under discussion. Fitzhugh (1976) states that the methods such as the use of residual variances may be subject to error due to correlations between longitudinal data points. Furthermore, the correlated effects may be stronger if seasonal effects are significant in determining weight at certain times. Allen (1967) as reported by Fitzhugh (1976) described a multivariate procedure appropriate for non-linear models assuming that observations on different animals at the same age were correlated. However, in data of the type analysed in this study such assumptions may not hold and in the analysis of biological data removing the correlated errors between longitudinal data points is difficult.

In the present analysis a pooled residual variance and mean prediction error estimate were used to calculate the fit of the functions assuming that the correlated errors between ages were removed in the weights predicted by the growth functions. The usual test of fit such as the sum of squares of the deviations $(Y-\hat{Y})^2$ or a mean square deviation was not used due to the inherent bias existing in this method of analysis which attributed an equal weighting when the observed weight was 50 kg and predicted weight 100 kg or when the observed weight was 500 kg and predicted weight 550 kg. Thus, a procedure using a relative fit or mean prediction error estimate was considered appropriate when

the fit of the four functions was to be evaluated. Brown et al. (1976) and Fitzhugh (1976) in addition to using residual variances, relied on visual comparisons of the fitted curves with the actual data at selected ages together with the biological interpretability of the fitted parameters as a measure of the accuracy of fit.

In studies comparing fitted parameters derived from growth functions applied to two breeds or sets of data the importance of the consistency in the error estimate has not been stressed in the literature. Thus, in an ideal situation not only must the function fit the two sets of data well but errors calculated at each age or overall ages must be consistent in order to make a reliable comparison of the fitted parameters such as (A) and (k) especially as they are negatively correlated. The present analysis showed the importance of the consistency of error when estimates of the same parameter based on a biological model is compared between two breeds or sets of data.

A knowledge of growth curves is important to scientists interested in lifetime trends. The application of growth curves to a part of the lifetime data does not provide accurate information about the growth patterns of an animal or population. Weight age data on each animal from birth to an appropriate adult weight should be available for a growth curve analysis.

In conclusion growth models offer a mathematical description of growth. The generalized Richards or the simpler Brody model can permit a detailed study of growth and its properties in beef cattle.

<u>References</u>

Averdunk, G. 1968. Genetic aspects of test period length for rate of gain in cattle. J. Anim. Sci. 27: 1124 abs.

Baker, G.A. 1944. Weight growth curves. Poult. Sc. 23: 83.

Bandy, J.P., Cowan, I.McT. and Wood, A.J. 1970. Comparative growth in 4 races of black tailed deer. I. Growth in body weight. Can. J. Zool. 48: 1401.

Berg, R.T. and Butterfield, R.M. 1976. New concepts of cattle growth. Sydney University Press.

Berg, R.T. 1971. University of Alberta beef breeding project. Report no. 6. 50th Annual Feeders' Day Report, Dept. Anim. Sci., University of Alberta, p 4.

Berg, R.T. 1973. University of Alberta beef breeding project. Report no. 7. 52nd Annual Feeders' Day Report, Dept. Anim. Sci., University of Alberta, p 25.

Berg, R.T. 1975. University of Alberta beef breeding project. Report no. 8. 54th Annual Feeders' Day Report, Dept. Anim. Sci., University of Alberta, p 30.

Bertalanffy, L. 1957. Quantitative laws in metabolism and growth. Quart. Review of Biol. 32: 217.

Brinks, J.S., Clark, R.T., Keiffer, N.M. and Urick, J.J. 1964. Estimates of genetic, environmental and phenotypic parameters in range Hereford females. J. Anim. Sci. 23: 711.

Brody, S. 1945. Bioenergetics and growth. Reinhold Publishing Corporation, N.Y. Chap. 16.

Brown, J.E. 1970. Comparison of five stochastic models on their ability to describe the weight-age relationships in cattle. ph.D. Thesis, Texas A & M. Abst. From Dissertation Abs. Int. 1971 V32 #1. p 96B.

Brown, J.E. 1970. A comparison of five stochastic models for describing weight age curves of cattle. J. Anim. Sci. 31: 161 abs.

Brown, J.E., Brown, C.J. and Butts, W.T. 1972a. A discussion of the genetic aspects of weight, mature weight and rate of maturing in Hereford and Angus cattle. J. Anim. Sci. 34: 525.

Brown, J.E., Brown, C.J. and Batts, W.R. 1972b. Relationships among measures of growth from birth to maturity in Hereford and Angus cattle. University of Arkansas Agric. Exp. Station Bull. 773. April.

Brown, J.E., Brown, C.J. and Butts, W.T. 1973. Evaluating relationships among immature measures of size, shape and performance of bulls, III. The relationship between post weaning test performance, size and shape at 12 months. J. Anim. Sci. 37: 11.

Brown, J.E., Fitzhugh, H.A., Jr. and Cartwright, T.C. 1976. A comparison of non-linear models for describing weight age relationships in cattle. J. Anim. Sci. 42: 810.

Byrne, G.F. 1973. An approach to growth curve analysis. Agric. Meteorology. 11: 161.

Calo, L.L., Dowell, R.E., Van Vleck, L.D. and Miller, P.D. 1973. Parameters of growth of Holstein Friesian bulls. J. Anim. Sci. 37: 417.

Calo, L.L., McDowell, R.E., Van Vleck, L.D. and Miller, P.D. 1973a. Genetic aspects of beef production among Holstein Friesians pedigree selected for milk production. J. Anim. Sci. 7: 676.

Causton, D.R. 1969. A computer program for fitting the Richards function. Biometrics 25: 401.

Cheek, D.B. 1968. Human growth. Body composition, cell growth energy and intelligence. Lea & Febiger Publ. Philadelphia.

Cock, A.G. 1966. Genetical aspects of metrical growth and form in animals. Quart. Review of Biology 41: 131.

Eisen, E.J. 1976. Growth curve analysis in mice and rats. J. Anim. Sci. 42: 1008.

Eisen, E.J., Lang, B.J. and Legates, J.E. 1969. Comparison of growth functions within and between lines of mice selected for large and small body weights. Theoret. and Applied Genet. 39: 251.

Fabens, J.A. 1965. Properties of fitting the Von Bertalanffy growth curve. Growth 29: 265.

Fitzhugh, H.A., Jr., Cartwright, T.C. and Temple, R.S. 1967. Genetic and environmental factors affecting the weight of beef cows. J. Anim. Sci. 26: 991.

Fitzhugh, H.A. and Taylor St. C.S. 1971. Genetic analysis of the degree of maturity. J. Anim. Sci. 33: 717.

Fitzhugh, H.A. 1972. Selection to change the shape of the growth curve of beef cattle. Texas Agric. Experim. Station. Progress report. 3122.

Fitzhugh, H.A. 1974. Analysis of growth curves and strategies in changing their shape. Paper presented at a symposium on growth curve analysis. ASAS July 29. 1974. Univ. of Maryland.

Fitzhugh, H.A. 1976. Analysis of growth curves and strategies in changing their shape. J. Anim. Sci. 42: 1036.

Fox, J.D. 1970. The genetic relationship of mature size and efficiency of production in sheep. Ph.D. Thesis, Ohio State. From Dissertation Abst. Int. July 1971. 32, #1. p 8B.

Gill, J.L. 1971. Analysis of data with heterogeneous variance: a review. J. Dairy Sci. 54: 369.

Gill, J.L. 1977. Multiple comparison of means when variance is not homogeneous. J. Dairy Sci. 60: 444.

Harvey, W.R. 1960. Least squares analysis with unequal subclass numbers. USDA. ARS Bull. 20.

Howard, A., McLaren, A., Michie, D. and Sander, G. 1955. Genetic and environmental influences on the secondary sex ratio in mice. J. Genet. 53: 200.

Huxley, Sir J.S. 1932. Problems of relative growth. Methuen and Co. Ltd., London.

Joandet, G.E. and Cartwright, T.C. 1969. Estimation of the efficiency of beef production. J. Anim. Sci. 29: 862.

Keeping, E.S. 1962. Introduction to statistical inference. D. Van Nostrand Co. Inc.

Kidwell, J.F., Howard, A. and Laird, A.K. 1969. Inheritance of growth and form in the mouse. II. The Gompertz growth equation. Growth 33: 339.

Laird, A.K., Tyler, S.A. and Barton, A.D. 1965. Dynamics of normal growth. Growth 29: 233.

Laird, A.K. 1965. Dynamics of relative growth. Growth 29: 249.

Laird, A.k. 1966. Post natal growth of birds and mammals.

Growth 30: 349.

Laird, A.K. and Howard, A. 1967. Growth curves in inbred mice. Nature 213: 786.

Lars-Erik Liljedahl. 1970. A study on the course of growth in broiler chickens. Acta Agric. Scand. 20: 249.

Lerner, I.M. and Asmundson, V.S. 1938. Genetic growth constants in the domestic fowl. Poult. Sci. 17: 286.

Lerner, I.M. 1939. Shape of the chick embryo growth curve. Science 89: 16.

Long, C.R., Cartwright, T.C. and Fitzhugh, H.A. 1975a. Systems analysis of sources of genetic and environmental variation in the efficiency of beef production - cow size and herd management. J. Anim. Sci. 40: 409.

Long, C.R., Cartwright, T.C. and Fitzhugh, H.A. 1975. Systems analysis of sources of genetic and environmental variation in the efficiency of beef production mating plans. J. Anim. Sci. 40: 433.

Marubini, E., Resele, L.F. and Barehini, G. 1971. A comparative fitting of the Gompertz and Logistic functions to longitudinal height data during adolescence in girls. Human Biol. 43: 237.

Morris, C.A. and Wilton, J.W. 1976. Influence of body size on biological efficiency of cows: a review. Can. J. Anim. Sci. 56: 613.

Nelder, J.A. 1961. Fitting of a generalization of the Logistic curve. Biometrics 17: 89.

Nelder, J.A. 1962. An alternate form of the generalized Logistic equation. Biometrics 18: 614.

Parks, J.R. 1970a. Growth curves and the physiology of growth I. Animals. Amer. J. Physiol. 219: 833.

Parks, J.R. 1970b. Growth curves and the physiology of growth II. Effects of dietary energy. Amer. J. Physiol. 219: 837.

Richards, J.F. 1959. A flexible growth function for empirical use. J. Expt. Botany 10: 290.

Ricklefs, R.E. 1967. A graphical method of fitting equations to growth curves. Ecology 48: 978.

Ricklefs, R.E. 1968. Patterns of growth in birds. Ibis, 110: 419.

Robinson, D.W. 1971. Cellular basis for changes in body composition. J. Anim. Sci. 33: 416.

Rutledge, J.J., Robinson, O.W., Eisen, E.J. and Legates, J.E. 1972. Dynamics of genetic and maternal effects in mice. J. Anim. Sci. 35: 911.

Shelby, c.E., Harvey, W.R., Clark, R.T., Queensberry, J.R. and Woodward, R.R. 1963. Estimation of phenotypic and genetic parameters in 10 years of Miles City R.O.P. steer data. J. Anim. Sci. 22: 346.

Smith, G.M., Fitzhugh, H.A., Cundiff, L., Cartwright, T.C. and Gregory, K.E. 1976a. Heterosis for maturing patterns in Hereford, Angus and Shorthorn cattle. J. Anim. Sci. 43: 380.

Smith, G.M., Fitzhugh, H.A., Cundiff, L., Cartwright, T.C. and Gregory, K.E. 1976b. A genetic analysis of maturing patterns in straightbred and crossbred Hereford, Angus and Shorthorn cattle. J. Anim. Sci. 43: 389.

Snedecor, G.W. 1962. Statistical methods. Iowa State College Press, Ames, Iowa.

Steel, G.D. and Torrie, J.H. 1960. Principles and procedures of statistics. McGraw-Hill Book Company, Inc. New York.

Swinger, L.A. and Hazel, L.N. 1961. Optimum length of feeding period in selecting for gain in beef cattle. J. Anim. Sci. 20: 189.

Tanner, J.M. 1955. Some notes on the reporting of growth data. Human Biol. 23: 93.

Taylor, St. C.S. 1965. The relation between mature weight and time taken to mature in animals. Anim. Prod. 7: 203.

Taylor, St. C.S. and Craig, J. 1965. Genetic correlations during the growth of twin cattle. Anim. Prod. 7: 83.

Taylor, St. C.S. 1968. Time taken to mature in relation to mature weight for sexes, strains and species of domesticated birds and mammals. Animal Prod. 10: 157.

Taylor, St. C.S. and Fitzhugh, H.A. 1971. Genetic relationships between mature weight and time taken to mature within a breed. J. Anim. Sci. 33: 726.

Timon, V.M. and Eisen, E.T. 1969. Comparison of growth curves in mice selected and unselected for post weaning gain. Theoret. and Applied Genet. 39: 345.

Vieira, S. and Hoffman, R. 1977. Comparison of the Logistic and Gompertz growth functions considering additive and multiplicative error terms. Applied Statistics 26: 143.

Appendix Table 1. Minima and maxima of mean prediction error (%) for unadjusted and adjusted Hybrid data by function and age

Age	Number of Animals	Function	Mean Prediction Error (%) Unadjusted Min. (%)	Unadjusted Max. (%)	Adjusted Min. (%)	Adjusted Max. (%)
Birth	203 [1]	Richards	-55.833	26.100	-99.742	24.386
		Brody	-85.501	12.756	-98.252	24.951
	454 [2]	Bertalanffy	-119.647	-4.162	-148.676	5.862
		Logistic	-225.497	-68.586	-305.786	-53.613
Weaning	203	Richards	-83.587	24.709	-86.665	30.838
		Brody	-69.734	29.756	-87.204	30.629
	439	Bertalanffy	-55.043	35.249	-70.232	37.180
		Logistic	-51.561	37.476	-58.532	41.345
Yearling	196	Richards	-64.760	24.982	-113.349	22.911
		Brody	-64.181	25.557	-113.294	22.963
	488	Bertalanffy	-64.664	25.768	-115.753	23.087
		Logistic	-59.990	28.300	-114.253	25.803
20 months	177	Richards	-16.063	26.360	-71.655	30.654
		Brody	-18.967	24.477	-71.519	30.706
	290	Bertalanffy	-23.284	21.758	-76.355	28.841
		Logistic	-27.043	19.290	-81.193	27.145
32 months	158	Richards	-48.673	19.667	-48.029	17.133
		Brody	-51.426	18.299	-47.964	17.218
	269	Bertalanffy	-53.493	17.414	-48.844	16.775
		Logistic	-55.663	16.456	-49.665	16.367
44 months	142	Richards	-32.656	25.946	-35.446	26.485
		Brody	-32.568	26.225	-35.495	26.455
	223	Bertalanffy	-30.255	27.653	-32.492	28.204
		Logistic	-29.015	28.421	-30.242	29.488
56 months adult	128	Richards	-22.902	28.029	-19.147	27.660
		Brody	-20.234	29.658	-19.260	27.589
	185	Bertalanffy	-15.758	32.330	-14.698	30.401
		Logistic	-13.584	33.618	-11.922	32.099

[1] Unadjusted
[2] Adjusted

Appendix Table 2. Minima and maxima of mean prediction error (%) for unadjusted and adjusted Hereford data by function and age

Age	Number of Animals	Function	Mean Prediction Error (%) Unadjusted Min. (%)	Unadjusted Max. (%)	Adjusted Min. (%)	Adjusted Max. (%)
Birth	144 [1]	Richards	-71.83	29.862	-73.428	28.828
		Brody	-84.33	24.763	-55.465	36.200
	319 [2]	Bertalanffy	-124.42	8.399	-100.328	17.789
		Logistic	-264.14	48.629	-222.859	-32.496
Weaning	144	Richards	-66.193	21.042	-73.813	30.856
		Brody	-61.209	23.086	-83.393	26.668
	307	Bertalanffy	-45.543	30.91	-61.743	35.954
		Logistic	-42.497	32.289	-52.337	38.739
Yearling	137	Richards	-60.254	25.488	-58.238	24.044
		Brody	-59.958	25.901	-57.305	24.778
	339	Bertalanffy	-59.148	27.312	-59.730	22.984
		Logistic	-54.761	30.208	-60.881	25.661
20 Months	126	Richards	-29.097	18.179	-41.781	26.414
		Brody	-30.299	17.447	-40.071	27.195
	206	Bertalanffy	-34.759	14.672	-44.203	25.239
		Logistic	-39.398	11.921	-49.045	23.142
32 Months	107	Richards	-43.228	24.422	-44.791	22.202
		Brody	-44.187	23.955	-44.197	22.554
	192	Bertalanffy	-46.432	22.952	-44.793	22.146
		Logistic	-48.709	21.955	-44.419	22.247
44 Months	89	Richards	-26.950	19.244	-31.384	19.489
		Brody	-26.78	19.390	-32.329	18.949
	147	Bertalanffy	-24.728	20.820	-29.275	20.734
		Logistic	-23.126	21.921	-25.975	22.706
56 Months	67	Richards	-26.733	21.625	-19.436	24.489
		Brody	-25.579	22.360	-21.275	23.371
	102	Bertalanffy	-20.707	25.425	-16.454	26.332
		Logistic	-17.688	27.310	-12.577	28.757

[1] Unadjusted
[2] Adjusted

Appendix Table 3. Mean prediction errors, standard deviations (Sd), standard errors (Se), minima and maxima by function and age - 100% BR

Age	No. of Animals	Function	Mean Prediction Error (%)	Sd. (%)	Se. (%)	Min. (%)	Max. (%)
Birth	34	Richards	1.633a	12.078	2.071	-32.873	20.565
		Brody	2.969a	11.914	2.043	-31.067	21.645
		Bertalanffy	-17.420b	14.417	2.473	-58.609	51.179
		Logistic	-87.896c	23.071	3.957	-153.806	-51.732
Weaning	34	Richards	-3.488a	11.371	1.950	-44.483	12.874
		Brody	-4.162a	11.418	1.958	-45.241	12.290
		Bertalanffy	4.938b	10.806	1.853	-24.800	20.167
		Logistic	11.378c	10.011	1.717	-25.346	25.639
Yearling	26	Richards	0.097a	8.566	1.188	-20.826	16.426
		Brody	0.151a	8.598	1.192	-20.891	16.418
		Bertalanffy	-0.828a	8.239	1.143	-20.188	16.369
		Logistic	-0.928a	7.944	1.102	-20.195	17.548
20 Months	23	Richards	0.908a	8.842	1.318	-19.319	15.729
		Brody	1.117a	8.823	1.315	-19.064	15.904
		Bertalanffy	-1.691ab	8.997	1.341	-22.503	13.381
		Logistic	-4.732b	9.114	1.359	-26.265	10.507
32 Months	25	Richards	-7.964a	11.693	2.339	-33.665	13.288
		Brody	-7.916a	11.686	2.337	-33.600	13.317
		Bertalanffy	-7.534a	11.669	2.334	-33.221	13.761
		Logistic	-6.283a	11.557	2.312	-31.754	14.888
44 Months	13	Richards	0.836a	7.925	2.198	-19.955	10.149
		Brody	0.690a	7.937	2.201	-20.128	10.020
		Bertalanffy	3.558a	7.711	2.139	-16.706	12.579
		Logistic	6.330b	7.492	2.078	-13.371	15.074
56 Months	12	Richards	3.469a	12.938	3.735	-21.619	23.906
		Brody	3.203a	12.972	3.745	-21.949	23.697
		Bertalanffy	7.263a	12.439	3.591	-26.873	26.892
		Logistic	10.342a	12.028	3.472	-13.005	29.319

a,b,c,d - Mean prediction error estimates with different alphabetic letters are significant $P<0.05$

Appendix Table 4. Mean prediction errors, standard deviations (Sd), standard errors (Se), minima and maxima by function and age - 75% BR

Age	No. of Animals	Function	Mean Prediction Error (%)	Sd. (%)	Se. (%)	Min. (%)	Max. (%)
Birth	56	Richards	0.016a	18.404	2.459	-68.081	26.995
		Brody	4.886a	17.508	2.340	-59.895	30.551
		Bertalanffy	-16.958b	21.529	2.877	-96.616	14.601
		Logistic	-85.309c	34.112	4.558	-211.522	-35.307
Weaning	56	Richards	-4.359a	16.614	2.220	-54.688	24.155
		Brody	-6.765a	16.828	2.249	-57.213	22.697
		Bertalanffy	3.104b	15.922	2.128	-46.502	28.818
		Logistic	9.469c	14.595	1.950	-36.008	33.963
Yearling	47	Richards	-0.124a	12.228	1.268	-37.332	20.878
		Brody	0.012a	12.321	1.278	-37.311	21.377
		Bertalanffy	-0.721a	12.000	1.244	-37.613	20.422
		Logistic	-0.392a	11.662	1.209	-35.808	21.884
20 Months	35	Richards	-0.561a	10.235	1.223	-29.833	18.617
		Brody	0.130a	10.167	1.215	-28.967	19.179
		Bertalanffy	-2.737a	10.412	1.244	-32.413	16.735
		Logistic	-5.881b	10.642	1.272	-35.989	13.939
32 Months	39	Richards	-6.621a	12.344	1.977	-32.998	16.578
		Brody	-6.529a	12.337	1.976	-32.936	16.693
		Bertalanffy	-6.063a	12.267	1.964	-32.115	16.862
		Logistic	-4.702a	12.098	1.937	-30.198	17.746
44 Months	22	Richards	-1.312a	12.344	1.977	-32.998	16.578
		Brody	-1.911a	12.448	2.654	-44.095	15.960
		Bertalanffy	1.320a	12.057	2.571	-39.477	18.630
		Logistic	4.442a	11.677	2.490	-35.043	21.207
56 Months	12	Richards	7.025a	9.397	2.713	-9.356	19.886
		Brody	6.049a	9.494	2.741	-10.484	19.041
		Bertalanffy	10.416a	9.058	2.615	-5.407	22.815
		Logistic	13.707a	8.727	2.520	-1.546	25.553

a,b,c,d - Mean prediction error estimates with different alphabetic letters are significant $P<0.05$

Appendix Table 5. Mean prediction errors, standard deviations (Sd), standard errors (Se), minima and maxima by function and age - 50% BR 50% LD

Age	No. of Animals	Function	Mean Prediction Error (%)	Sd. (%)	Se. (%)	Min. (%)	Max. (%)
Birth	28	Richards	0.881a	8.778	1.661	-13.760	19.564
		Brody	1.451a	8.738	1.651	-13.105	20.027
		Bertalanffy	-18.839b	10.537	1.991	-36.392	3.561
		Logistic	-89.582c	16.808	3.176	-117.583	-53.847
Weaning	28	Richards	-2.281a	14.537	2.747	-54.973	16.024
		Brody	-2.551a	14.580	2.755	-55.460	15.747
		Bertalanffy	6.268b	13.263	2.507	-39.787	24.571
		Logistic	12.154c	12.379	2.339	-32.073	28.391
Yearling	23	Richards	-1.910a	14.280	2.105	-55.144	19.899
		Brody	-1.895a	14.290	2.107	-55.176	19.897
		Bertalanffy	-2.690a	14.036	2.070	-54.396	19.782
		Logistic	-1.628a	13.575	2.002	-49.651	21.562
20 Months	17	Richards	0.785a	9.448	1.620	-20.016	17.208
		Brody	0.871a	9.439	1.619	-19.911	17.279
		Bertalanffy	-2.023a	9.683	1.661	-23.521	14.760
		Logistic	-5.065a	9.965	1.709	-27.338	12.144
32 Months	16	Richards	-5.125a	11.707	2.686	-26.423	14.974
		Brody	-5.099a	11.704	2.685	-26.393	14.993
		Bertalanffy	-4.858a	11.704	2.685	-26.082	15.287
		Logistic	-4.264a	11.665	2.676	-25.346	15.898
44 Months	13	Richards	-3.612a	12.548	3.480	-26.412	15.325
		Brody	-3.671a	12.556	3.482	-26.489	15.276
		Bertalanffy	0.559a	12.161	3.373	-22.527	17.838
		Logistic	1.920a	11.854	3.288	-19.433	19.872
56 Months	6	Richards	7.656a	6.585	2.688	1.840	19.481
		Brody	7.550a	6.592	2.691	1.726	19.388
		Bertalanffy	11.718a	6.299	2.572	6.166	23.034
		Logistic	14.371a	6.111	2.495	8.988	25.350

a,b,c,d - Mean prediction error estimates with different alphabetic letters are significant P<0.05

Appendix Table 6. Mean prediction errors, standard deviations (Sd), standard errors (Se), minima and maxima by function and age - 75% LB

Age	No. of Animals	Function	Mean Prediction Error (%)	Sd. (%)	Se. (%)	Min. (%)	Max. (%)
Birth	21	Richards	1.717a	11.463	2.502	-22.431	17.492
		Brody	-0.743a	11.750	2.564	-25.496	15.427
		Bertalanffy	-21.003b	14.113	3.080	-50.733	-1.581
		Logistic	-95.701c	22.825	4.981	-143.784	-64.289
Weaning	21	Richards	-4.444a	10.746	2.345	-23.659	17.925
		Brody	-3.230a	10.627	2.319	-22.340	19.024
		Bertalanffy	5.232b	9.863	2.152	-13.043	26.588
		Logistic	10.786b	9.238	2.016	-5.953	30.407
Yearling	16	Richards	0.539a	8.322	1.449	-19.319	15.702
		Brody	0.804a	8.309	1.946	-19.359	15.524
		Bertalanffy	-0.289a	8.340	1.452	-20.319	13.695
		Logistic	0.974a	8.470	1.474	-18.567	16.515
20 Months	14	Richards	0.801a	8.182	1.546	-16.553	16.947
		Brody	0.422a	8.217	1.553	-17.002	16.624
		Bertalanffy	-2.597a	8.451	1.597	-20.614	14.135
		Logistic	-5.572a	8.710	1.646	-24.197	11.638
32 Months	14	Richards	-6.543a	13.384	3.577	-27.377	16.023
		Brody	-6.697a	13.403	3.582	-27.554	15.910
		Bertalanffy	-6.715a	13.400	3.581	-27.511	15.977
		Logistic	-6.372a	13.353	3.569	-27.041	16.321
44 Months	10	Richards	-1.843a	10.477	3.313	-18.319	13.150
		Brody	-1.625a	10.459	3.308	-18.085	13.344
		Bertalanffy	1.194a	10.198	3.225	-14.933	15.801
		Logistic	3.437a	9.981	3.156	-12.385	17.737
56 Months	7	Richards	2.849a	14.090	5.326	-20.259	19.876
		Brody	3.317a	14.030	5.303	-19.708	20.257
		Bertalanffy	7.490a	13.461	5.088	-14.682	23.673
		Logistic	10.131a	13.086	4.946	-11.445	25.845

a,b,c,d - Mean prediction error estimates with different alphabetic letters are significant $P<0.05$

Appendix Table 7. Duncan's test between mean prediction error estimates at 7 ages based on four growth functions - 100% BR

Function	Birth	Weaning	Yearling	20 Mon.	32 Mon.	44 Mon.	Maturity
Richards	1.633b	-3.488ab	0.097b	0.908b	-7.964a	0.836b	3.469b
Brody	2.969b	-4.162ab	0.151b	1.117b	-7.916a	0.690b	3.203b
Bertalanffy	-17.420a	4.938d	-0.828c	-1.691c	-7.534b	3.558cd	7.263d
Logistic	-87.896a	11.378d	-0.928bc	-4.732b	-6.283b	6.330cd	10.342d

Mean prediction errors with different alphabetic letters in rows are significant $P<0.05$

Appendix Table 8. Duncan's test between mean prediction error estimates at 7 ages based on four growth functions - 75% BR

Function	Birth	Weaning	Yearling	20 Mon.	32 Mon.	44 Mon.	Maturity
Richards	0.016bc	-4.359ab	-0.124bc	-0.561bc	-6.621a	-1.312abc	7.025c
Brody	4.886b	-6.765a	0.012b	0.130b	-6.529a	-1.911ab	6.049b
Bertalanffy	-16.958a	3.104cd	-0.721bc	-2.737b	-6.063b	1.320bcd	10.416d
Logistic	-85.309a	9.469d	-0.392bc	-5.881b	-4.702bc	4.442cd	13.707d

Mean prediction errors with different alphabetic letters in rows are significant $P<0.05$

Appendix Table 9. Duncan's test between mean prediction error estimates at 7 ages based on four growth functions - 50% BR 50% LD

Function	Birth	Weaning	Yearling	20 Mon.	32 Mon.	44 Mon.	Maturity
Richards	0.881a	-2.251a	-1.910a	0.785a	-5.125a	-3.612a	7.656a
Brody	1.451a	-2.551a	-1.895a	0.871a	-5.099a	-3.671a	7.550a
Bertalanffy	-18.839a	6.268c	-2.690b	-2.023b	-4.858b	-0.559bc	11.718c
Logistic	-89.582a	12.154c	-1.628b	-5.065b	-4.264b	1.920bc	14.371c

Mean prediction errors with different alphabetic letters in rows are significant $P<0.05$

Appendix Table 10. Duncan's test between mean prediction error estimates at 7 ages based on four growth functions - 75% LB

Function	Birth	Weaning	Yearling	20 Mon.	32 Mon.	44 Mon.	Maturity
Richards	1.717a	-4.444a	0.539a	0.801a	-6.543a	-1.843a	2.849a
Brody	-0.743a	-3.230a	0.504a	0.422a	-6.696a	-1.625a	5.317a
Bertalanffy	-21.003a	5.232c	-0.289bc	-2.597b	-6.715b	1.194bc	7.490c
Logistic	-95.701a	10.786d	0.974bc	-5.572b	-6.372b	3.437bcd	10.131cd

Mean prediction errors with different alphabetic letters in rows are significant $P<0.05$

Appendix Table 11. Correlations between growth parameters from the Richards model fitted to the unadjusted Hybrid data (above diagonal) and Hereford data (below diagonal)

	(A)	(B)	(k)	(M)	(AGR12)
(A)	-	0.51	-0.70	-0.51	-0.15
(B)	0.56	-	-0.85	-0.97	-0.56
(k)	-0.86	-0.78	-	0.89	0.66
(M)	-0.62	-0.97	0.84	-	0.68
(AGR12)	-0.44	-0.56	0.71	0.67	-

All correlations were significantly different P<0.01

Appendix Table 12. Mean gains over period (kg) and differences $(Y-\hat{Y})$ by function and breed group

Function	Mean gain over period kg							
	Birth-Wean		Wean-Yrl.		Yrl.-18 Mon.		18 Mon.-Adult	
	HY	HE	HY	HE	HY	HE	HY	HE
Observed (Y)	149.802	125.549	81.948	91.657	127.749	112.799	99.947	98.904
Richards (YR)	142.602	119.149	100.364	99.642	75.646	77.780	123.159	110.093
Brody (YB)	142.602	132.240	99.705	92.543	75.132	71.683	124.180	122.348
Bertalanffy (YV)	116.829	106.803	114.209	105.970	87.228	84.023	96.729	96.519
Logistic (YL)	80.690	74.346	113.448	106.868	106.163	102.836	77.887	73.097
Difference $(Y-\hat{Y})$								
Y-YR	7.200	6.400NS	-18.416	-7.985	52.103	45.019	-23.212	-11.189NS
Y-YB	7.200	-6.691NS	-17.757	-0.886NS	52.617	51.116	-24.233	-23.444
Y-YV	32.973	18.746	-32.261	-14.313	40.521	38.776	3.218NS	2.385NS
Y-YL	69.112	51.203	-31.500	-15.211	21.586	19.963	22.063	25.807

All differences $(Y-\hat{Y})$ were significant at P<0.01 except the values denoted by a NS

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